SHORELINE DISTRIBUTION AND LANDSCAPE GENETICS OF BEARS IN A RECENTLY DEGLACIATED FJORD: GLACIER BAY, ALASKA

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A

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Abstract

To further knowledge of mammalian colonization patterns following deglaciation, I used occupancy modeling to estimate black and brown bear shoreline distribution of Glacier Bay and how these distributions relates to the number years of land exposure and post glacial plant and stream succession. I also conducted microsatellite genetic analysis of brown bear hair and tissue to determine contemporary population structure throughout the park and how it relates to landscape features and surrounding populations. Closed forest cover within 1 km of the study site was a strong positive predictor of black bear occurrence. Brown bears were detected at 100% of sites although their use was highest in recently glaciated and old growth forest areas, and lowest in young forests. The shoreline of Glacier Bay hosts brown bears from three geographically overlapping distinct populations, one of which is likely composed of the original colonizers following glacial retreat that were isolated long enough to undergo genetic drift. The southern portion of Glacier Bay fjord and the Fairweather Mountain range are barriers to dispersal. Evidence of range expansion and recent migration indicate that brown bears are still actively colonizing Glacier Bay.

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Introduction

"*Glacier Bay in Southeast Alaska…provides a unique opportunity for studying the various phenomena associated with shrinking glaciers and the emergence from under the ice of new land and marine features. Here is offered an example on a small scale of conditions which have prevailed many times in geologic history during the waning of the continental ice sheets which in future may affect millions of square miles of the earth's surface now buried beneath glacial ice.*" - William O. Field, Jr. 1947 (in Brown 1982).

The biogeographic history of northern Southeast Alaska is complex and dynamic due to repeatedly advancing and retreating glaciers and changing sea level throughout the Pleistocene and into the Holocene. The three major forces of glaciation, tectonism, and isostacy have repeatedly altered the landforms and waterways in this region, often moving, burying, or submerging any geologic or fossil evidence that might have helped decipher the chronology of the land and its inhabitants (Mann 1986). Still, based on current geologic and biologic features we can infer the timing and extent of the last glacial maximum (LGM) as well as the more recent little ice age (LIA). From present topography and bathymetry we can estimate historic sea levels at times when more or less of the oceans' water was taken up in ice. From contemporary plant and animal distributions combined with genetic analysis of diversity and relatedness to surrounding populations, we can begin to tease out source populations, migration routes, and potential glacial refugia.

In this thesis I explore the biogeographic past by examining the contemporary distribution of ursid species and by assessing the landscape genetics of bears in Glacier Bay, at the northern extent of the Alexander Archipelago. While this examination will be limited in taxa, my hope is that learning how these two vagile megafaunal species have distributed themselves across the landscape will shed light into the mystery of past, present and future mammalian species distribution in SE Alaska.

Study area

Glacier Bay National Park and Preserve (GLBA) encompasses 13,289 km^2 in northern Southeast Alaska (Fig. 0.1). Glacier Bay is a deep marine fjord that extends 100 km from Icy Strait northward. The climate is characterized by cool summers and wet winters, and topography consists of rugged mountains up to 4,633 m elevation, icefields with glaciers extending to tidewater, and glacially carved mountains and valleys (Boggs et al. 2008). The study area encompasses Glacier Bay and surrounding landscape features, including the lower portion of glacially-fed Alsek River, Gulf of Alaska shoreline, Icy Strait shoreline, and the shoreline areas surrounding the Chilkat and Fairweather Mountain Ranges. The majority of the alpine zone in this remains covered in ice fields. Resident human population in the area is sparse and restricted to a single town (Gustavus, population ~400) including the National Park headquarters along the southern boundary. The rest of the study area is essentially devoid of human development. While the shoreline of Glacier Bay receives a limited amount of human recreational use in summer (750-1500backcountry visitors annually) the marine waters of Glacier Bay receive over 400,000 visitors via motorized vessel, mainly cruise ships. (NPS unpublished data). Access to the park is by airplane or boat. For the landscape genetics portion of this thesis (Chapter 2), I considered a larger study area of 37,017km^2 area in northern Southeast Alaska including Glacier Bay National Park and Preserve (GBNPP) and adjacent mainland United States National Forest (USFS), British Columbia Park, and private lands to the north and east (Fig. 1). The study area encompasses a wide variety of landscape features, including: the Yakutat forelands and lower portion of the large glacial-fed Alsek River on the north, Gulf of Alaska shoreline on the west, Icy Strait shoreline on the south, Chilkat Mountains and Lynn Canal on the east, and the Fairweather Mountain Range and Glacier Bay in the center. The study area encompasses the villages of Yakutat and Gustavus (<500 people each), seasonal tourism in Glacier Bay, and small (<20 people) seasonal fish camps along the Gulf of Alaska coast north of the park. The rest of the study area is essentially devoid of human development.

The lowlands that are presently Glacier Bay fjord were almost entirely filled during an ice advance culminating approximately 260 years ago (Connor et al. 2009). This advance was followed immediately by catostophic retreat over the next two hundred years (Lawrence 1958), exposing new fjords and new ground available for plant and animal recolonization. Glacier Bay now represents a 260-year successional chronosequence from barren tidewater glaciers near the heads of the fjord to late-seral forests near the mouth of the bay. The chronosequence of successional stages documented in Glacier Bay includes: pioneer communities of algae/lichen, seral forbs, and *Dryas drummondii* in areas glaciated within 50 ybp; open and closed scrub from 50-100 ybp; young forests from 100-300 ybp; and a climax community of old growth forests with *Sphagnum* muskegs in areas that remained ice-free during the LIA (Chapin et al. 1994). Early pioneer stage plants offer few food resources to bears, but open scrub habitats often contain a mosaic of bear foods including soapberry (*Shepherdia Canadensis*, strawberry (*Fragaria chiloensis*), locoweed (*Oxytropis campestris*), and bear root (*Hedysarum alpinum*). Closed scrub habitats dominated by willow (*Salix* spp.) often contain extensive soapberry, while alder-dominated (*Alnus* spp.) closed scrub contains little high-quality bear forage with the exception of groundcone (*Boschniakia rossica*), an alder root parasite (Pojar et al. 1994). Young forests in the southern portion of the Glacier Bay are dominated by dense (>60% canopy cover) Sitka spruce (*Picea sitchensis*) with little understory. Several berry-producing species including blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and red elderberry (*Sambucus racemosa*) grow in limited abundance in young forest openings and fringe. Areas surrounding Glacier Bay that were not glaciated during the LIA consist of old-growth hemlock (*Tsuga heterophylla*) and spruce forests with interspersed peat muskegs. Old growth communities often contain dense understories of berry-producing plants including blueberry, salmonberry and devil's club berries (*Oplopanax horridus*). Skunk cabbage (*Lysichiton americanus*) is also common in wet areas. Old growth forests are open (<60% canopy cover) or closed, and support important spring sedge (*Carex* spp.) habitat. Riparian zones host seasonal anadromous fish runs that increase in diversity with number

of years since glaciation (Milner et al. 2000). A large portion of the coastline throughout the area is bordered by recently uplifted graminoid and herbaceous beach meadows. Bear food resources in these meadows include strawberry, nagoonberry (*Rubus arctica*), dandelion (*Taraxicum* spp.), horsetail (*Equisetum* spp.), angelica (*Angelica lucida*), cow parsnip (*Heracleum lanatum*), beach lovage (*Ligusticum hutenii*), pacific hemlock-parsley (*Conioselium chinense*), and grasses. In addition to the diversity of bear plant foods available, intertidal food sources available to bears along the shoreline include acorn barnacles (*Balanus* spp.), mussels (*Mytilus trossulus*), and rock gunnels (*Stichaedae/Pholidae*). Other potential prey species throughout the study area include moose (*Alces alces*), mountain goats (*Oreamnos americanus*), voles (*Myodes* and *Mycrotus* spp.), and ground-nesting birds.

Previous research

Brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) have recolonized Glacier Bay since the LGM and the LIA. Until relatively recently, it was believed that brown bears colonized Southeast Alaska from the north, and black bears from the south after the end of the last great ice age ~10,000 years ago (Klein 1965). However, black and brown bear fossils found in caves on Prince of Wales Island in the 1990s dated up to 40,000 years old indicate that both species coexisted in the area through at least part of the Late Wisconsin glaciation, thus further substantiating the theory that a habitable coastal refugia existed in Southeast Alaska during this time (Heaton et al. 1996). Recent mitochondrial DNA analysis of permafrost-preserved brown bear tissue found that the haplotypes of all four northwestern North American clades were present in interior Alaska 13,000-42,000 years ago, indicating that brown bear populations survived the LGM in isolated refugia (Leonard et al. 2000). Through lineage sorting and founder effect, these small populations likely became dominated by the haplotypes seen today such as the unique haplotypes found on Admiralty, Baranof, and Chichagof (ABC) Islands (Talbot and Shields 1996, Leonard et al. 2000).

While few records of black bears exist from the early 1900's, brown bears were recorded in Glacier Bay by John Muir (NPS 2009). Prior to this study, it was believed that black bears tend to live in the forested areas of the lower bay, while brown bears dominate in the more open upper reaches of the bay (NPS 2009). Population size, home range size, movements, and distribution of each species in the park are not known. Habitat usage of bears in Glacier Bay was studied by Partridge et al. (2009) in eight select study areas from 2005-2006. Additionally nine hair samples collected from brown bears in Glacier Bay were analyzed for stable isotopes revealing a largely vegetarian diet of 69% plant material, 31% marine derived, and 0% terrestrial meat (Mowat and Heard 2006). No population demographic or movement data has been collected for either species in the study area.

Management need

Glacier Bay is a dynamic landscape resulting from both natural processes such as retreating glaciers leading to species colonization and succession, as well as anthropogenic changes such as climate change and increasing human use. Species such as bears that are dependent on shoreline habitats must adapt rapidly to changes in food types and abundance as well as human disturbance and use patterns over a relatively short period of time. Brown bears have historically been and continue to be species of special management concern in Glacier Bay. Glacier Bay National Monument (established in 1925), was significantly expanded in 1939 to create a brown bear sanctuary due to public outcry over questionable state game management laws (Catton 1995). Brown bears also have one of the lowest reproductive rates of any terrestrial mammal (Bunnell and Tait 1981). In addition, brown bears in Glacier Bay must adapt to ecological changes at faster rates than most other species for the following reasons: 1) brown bears are believed to occupy the peri-glacial areas where the landscape changes occur most rapidly, 2) they occupy areas of open and steep terrain surrounded large ice fields where beach habitats are likely essential to survival, 3) they often occupy shoreline areas of the park where visitors concentrate, and 4) overall numbers in Glacier Bay proper are likely relatively low due to limited availability of habitat.

This project examined current black and brown bear distribution in Glacier Bay and how this distribution relates to the number years of land exposure, as well as post glacial plant and stream succession. I also examined microsatellite genetic analysis of brown bear hair and tissue to determine contemporary population structure throughout the park and how it relates to landscape features and surrounding populations. Results of this study provide insights into the relationship between landscape changes and ursid colonization that will allow future projections and associated management.

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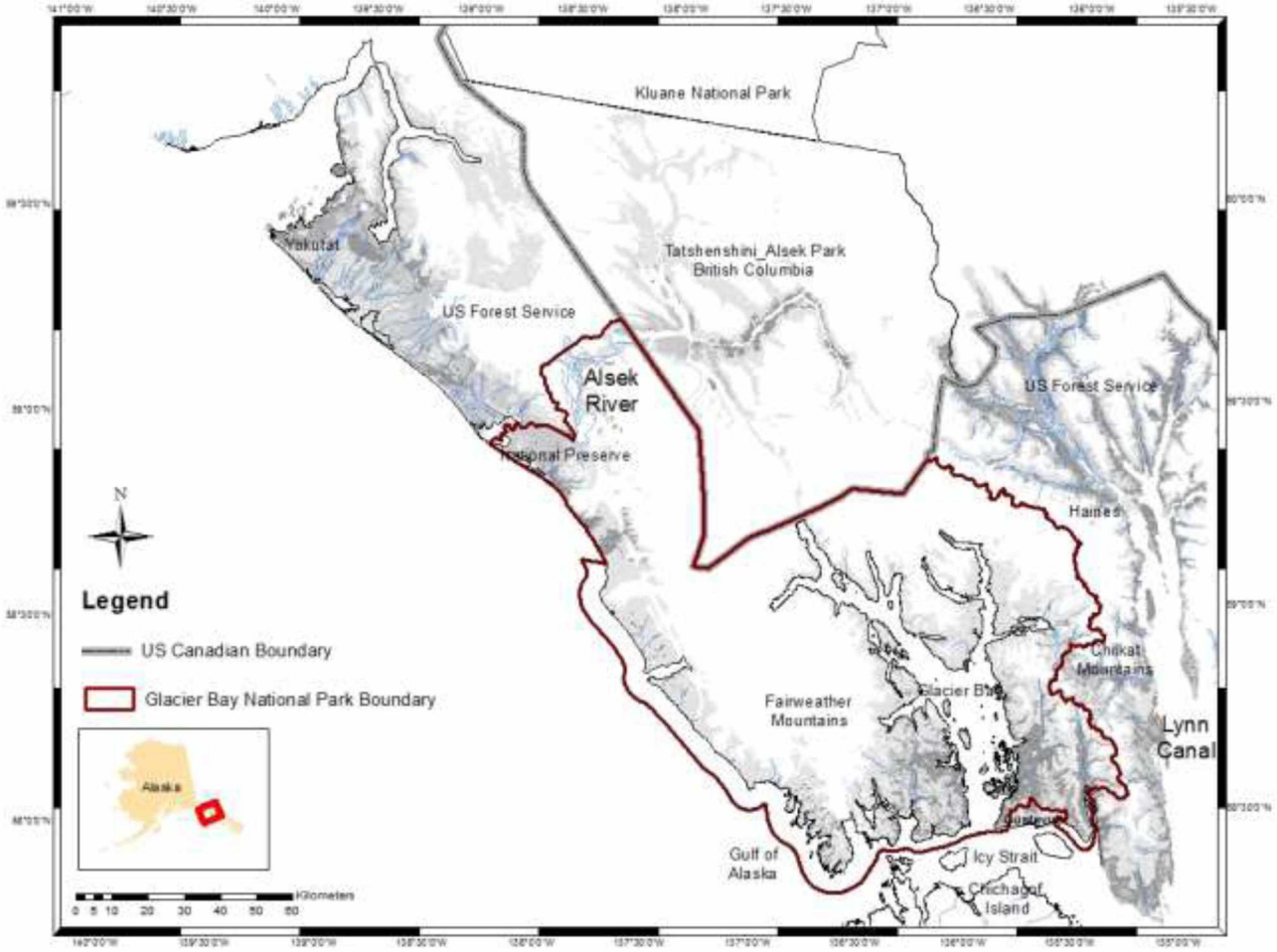

Fig. 0.1. Location of study area for bear distribution and brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010.

Chapter 1: Contemporary shoreline distribution of brown and black bears at a recently deglaciated Alaskan fjord: insights into recolonization and interspecific competition

Abstract

Southeast Alaska has a complex history of advancing and retreating glaciers and changing sea level throughout the Pleistocene and into the Holocene. Rapid ice retreat in Glacier Bay since the end of the Little Ice Age has exposed new ground for terrestrial species to recolonize from surrounding ice-free areas. The objective of this study was to establish current distributions of two recent colonizing mammals, black (*Ursus americanus*) and brown (*Ursus arctos*) bears, and examine how their distributions relate to successional habitat variables and interspecific competition. Bear species were detected non-invasively using visual observations, tracks, and genetic analysis of hair during 2-7 repeat surveys at forty shoreline sites in Glacier Bay National Park from 2009-2010. I tested single-season occupancy models to determine occurrence while accounting for imperfect and heterogeneous detection probabilities and used model selection to determine factors influencing detection and occurrence. Tracking substrate for brown bears and number of bear mark trees for black bears affected detection probabilities. Closed forest cover within 1 km of the study site proved to be a strong positive predictor of black bear occurrence. Brown bears were detected at 100% of sites so no occupancy or co-occurrence models could be generated. Brown bear use was highest in recently glaciated and old growth forest areas, and lowest in young forests. Brown bears appear to be currently expanding their range into southern Glacier Bay and the town of Gustavus, possibly in a second wave of colonization. Education for residents and visitors regarding food storage and brown bear behavior is important to minimize bear-human conflicts.

Introduction

Large-scale climate oscillations over the past two million years have had tremendous effects on land forms and species composition in the Northern Hemisphere. Massive ice sheets have repeatedly expanded and contracted causing catastrophic natural disturbance that expelled or killed virtually all species in the glacial path (Platt and Connell 2003). As the ice retreats, the resulting denuded surfaces are available for incremental and dynamic recolonization which involves large changes in species composition over time until a mature community is reached. The process of directional replacement of species along single or multiple pathways after a catastrophic natural disturbance is known as primary succession. Distributions of plants and animals after deglaciation are a result of the historical disturbance patterns of the landscape, the physiological tolerances and ecological requirements of the species, and interspecific interactions.

Southeast Alaska was repeatedly covered with glaciers during the Pleistocene until the retreat of the Cordilleran Ice Sheet approximately 12,000 years ago (Mann and Hamilton 1995). With the exception of individual plants and animals that may have survived in glacial refugia (Carrara et al. 2007, Heaton et al. 1996), all recolonization of this area has occurred since the last glacial maximum (LGM). Many areas of northern Southeast Alaska were covered again by ice during the Little Ice Age (LIA) 300-500 years ago. The lowlands that are presently Glacier Bay fjord were almost entirely filled during an ice advance culminating approximately 260 years ago (Connor et al. 2009). This advance was followed immediately by catastrophic retreat over the next two hundred years (Lawrence 1958), exposing new fjords and new ground available for plant and animal recolonization (Fig. 1.1). Plant and stream successional patterns have been well documented in Glacier Bay (Chapin et al. 1994, Chapin et al. 1995, Fastie 1995, Sharman et al. 1995, Milner et al. 2000, Milner et al. 2008,). Glacier Bay represents a 260-year successional chronosequence from barren tidewater glaciers near the heads of the fjord to late-seral forests near the mouth of the bay. Across this chronosequence, Chapin et al. (1994) found that life-history traits of colonizers (dispersal capability and generation time) determine the pattern of succession while initial site conditions and

species interactions (facilitation and competition) influence the rate of change and composition in plant communities over time. Early colonizing plants with long-distance seed dispersal and short generation times help develop the soil necessary for shrubs and trees, which then often outcompete the original colonizers. Milner et al. (2008) found that stream colonization, although initially influenced by water temperature and channel stabilization, became largely influenced by life-history traits of the colonizing species as well as tolerance among species. Colonizing species often remain present in the streams as they mature and diversity increases over time. Both terrestrial and stream systems exhibit multiple pathways of post-glacial succession due to life history traits, species interactions of colonizers, differences in abiotic environmental variables (such as landscape position, climate, stream water temperature, etc.), and proximity of colonizing populations (Chapin et al. 1994, Chapin et al. 1995, Fastie 1995, Sharman et al. 1995, Milner et al. 2008, Milner et al. 2000). Successional patterns of higher vertebrates have not been studied in Glacier Bay. Studies on post-fire mammalian recolonization have found that while vegetation type and density played a causal role in mammal successional patterns, herbivory from recent colonizers also affected the plant successional patterns by allowing unbrowsed species competitive advantage (Mills 1986, Fox et al. 2003).

In this study I investigated how post-glacial successional stage, life history traits, and species interactions affect the distribution of two recent mammalian colonizers in Glacier Bay. Brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) are two of the 29 terrestrial mammalian species that have re-colonized parts or all of Glacier Bay since the LIA (Taylor 1984). The distributions of many species have changed over the past 100 years, including those of brown and black bears. For example, brown bears were first recorded in Glacier Bay in the early 1900's (NPS 2009). They were commonly reported in Gustavus (Fig. 1.1) in the 1920s and 30s, but were likely exterminated by homesteaders and remained essentially absent in these areas from the 1960s through the late 1990s (NPS 2009). Conversely, black bears were more prevalent on the southern coast of the Gulf of Alaska in the 1960s and 1970s (Streveler 1974, 1975) and are rarely seen today (NPS 2009). Previous studies (NPS 2009, Partridge et al. 2009) and anecdotal

reports of bear sightings from 1900-2001 indicate that black bears predominate in the forested regions of southern Glacier Bay, while brown bears predominate in the more recently deglaciated areas in the northern part of the bay and along much of the outer coast (Gulf of Alaska), with wide mixing zones of the two species in the mid portions of Glacier Bay and in bays and inlets along Icy Strait and the outer Gulf of Alaska coast (Fig. 1.1). Changes in brown and black bear distributions over time would have been expected as the receding glaciers provided animals access to new territory. The current distribution of bears in Glacier Bay is likely related to food resources available in various plant and stream successional states, as well as life history traits and interactions among species.

Previous studies have shown substantial variation in the ecological communities that comprise bear habitat across the chronosequence. Partridge et al. (2009) found that although diversity of plants important for bear is highest in mature forest habitats, periglacial scrub habitats contain high proportions of alternative species, which may have particular importance to brown bears (NPS 2009). Several plant species found in recently deglaciated areas are believed to be important food resources to brown bears in Glacier Bay (NPS 2009), including bear root (*Hedysarum alpinum*), locoweed (*Oxytropis campestris*), and soapberry (*Shepherdia Canadensis)*, a particularly high-energy berry (Robbins et al. 2004). These plants exist in communities 50-150 years post-deglaciation, suggesting a moving front of foraging resources that subsequently diminish as the landscape develops into structurally more complex, but less productive vegetation communities, such as young forests (NPS 2009). The abundance and diversity of fish communities has been found to be positively correlated with stream age (Milner et al. 2000), suggesting salmon availability increases with the number of years since deglaciation. Anadromous fish may colonize streams with stable channels in less than 100 years but may require over 200 years to colonize streams with unstable channels (Sharman et al. 1995, Milner 2000). Unlike salmon resources, intertidal communities have been found to develop from early pioneer stage to maturity within 10 years when inhibitory conditions were removed experimentally (Sharman et al. 1995).

Colonization potential is affected by life history traits of black and brown bears that vary widely between species and sexes, as well as across age and geographic locations (Glenn and Miller 1980, McLoughlin et. al 1999, Koehler and Pierce 2003). While there is no information on population demographics of either species in Glacier Bay, in other regions of North America black bears generally have higher densities with smaller home ranges compared to brown bears (Table 1.1). Both black and brown bear dispersal patterns are strongly male-biased, with females usually remaining within their mothers' home ranges while males disperse outside of these natal ranges (Glenn and Miller 1980, Rogers 1987, Blanchard and Knight 1991, Schwartz and Franzmann 1992, Swenson et al. 1998, Lee and Vaughan 2003, Proctor et al. 2004). Due to shorter birth intervals and higher densities, black bear productivity can be12-22 times higher in number of cubs per year per 100 km^2 than brown bears (Mattson et al. 2005).

Differences between black and brown bear demographics and life history traits may contribute to interspecific competition and segregation, which in turn could affect the distribution and the dynamics of colonization potential. Brown bears are generally 1.6-2.3 times larger than black bears and have longer claws and more highly developed shoulder muscles, presumably evolved to allow them to effectively dig plant roots thus providing food sources unavailable to black bears (Herrero 1985, Mattson 1998). Black and brown bears have been found to exhibit dietary and temporal segregation in areas in which they overlap (MacHutchin et al. 1995, Jacoby et al. 1999, Fortin et al. 2007). Fortin et al. (2007) found that assimilated diets analyzed with stable isotopes for black and brown bears on the Kenai Peninsula from 2002-2004 were 83.6% plant and 79.9% animal matter, respectively. They concluded that brown bear presence on salmon streams virtually eliminated the use of salmon by black bears, despite estimated brown bear densities one tenth the density of black bears. Jacoby et al. (1999) also found reduced dietary overlap between the sympatric species, with black bears becoming more herbivorous in the presence of brown bears. In the Khutzeymateen Valley of British Columbia, MacHutchin et al. (1995) found with remote camera surveys that black bears were active at night while brown bears were active by day. Black bears were detected as

often as brown bears at certain fishing locations, but predominantly at night when fishing was presumed to be most difficult. These results contrasted to those from the Nimpkish Valley where allopatric black bears were active by day. The authors concluded that black bears avoided dominant brown bears in the Khutzeymateen by adjusting their temporal activity patterns. Brown bears, with bigger size and nutritional requirements, appear to dominate higher-quality concentrated food sources such as spawning salmon through interference or resource defense competition. Black bears may have an advantage in areas of widely dispersed food resources such as forbs and berries because of their smaller body sizes (lower nutritional requirements) and higher densities through scramble or exploitation competition (Mattson et al. 2005).

Objectives

The purpose of this study was to establish current distributions of black and brown bears and thereby test for the effects of successional history on their occurrence in periglacial ecosystems, as well as evaluate interactions between these two species. More specifically, I tested the following hypotheses: 1) the probability of occurrence of black and brown bears is not random across the landscape but rather is affected by the number of years since deglaciation and associated environmental covariates, 2) brown bears occur only in recently glaciated (<150 ybp) and old-growth forest (>260 ybp) areas because retreating glaciers provide a moving front of brown bear habitat that then diminishes as young forests (150-260 ybp) develop (NPS 2009), and young forests may not contain enough food resources to support brown bears experiencing exploitation competition from black bears (Mattson et al. 2005), 3) black bears occupy only young forest sites because black bears cannot utilize food resources (ie., roots) in recently glaciated areas, and resource defense competition from brown bears prevents black bears from colonizing old growth areas (Mattson et al. 2005), and 4) the detection probabilities of black bears are lower on a given survey in the presence of brown bears because of avoidance of the dominant species by the subordinate species (MacHutchon et al. 1995).

An important practical outcome of the study was establishment of a baseline for future monitoring of bear distribution. To facilitate this, a key methodological contribution was development of an occupancy-based distribution models that accounted for imperfect detectability and species interactions. This model will serve three functions: 1) comparison of changes in species distribution over time; 2) a better understanding of the effects of climate and successional changes in habitat on black and brown bear occurrence in periglacial and/or subarctic regions; and 3) allow prediction of future bear distribution based on projected landscape models to minimize bear-human conflicts when developing management plans, educational strategies, regulations, and/or planning infrastructure.

Methods

Study area

Glacier Bay National Park and Preserve (GLBA) encompasses 13,289 km^2 in northern Southeast Alaska (Fig. 1.2). Glacier Bay is a deep marine fjord that extends 100 km from Icy Strait northward. The climate is characterized by cool summers and wet winters, and topography consists of rugged mountains up to 4,633 m elevation, icefields with glaciers extending to tidewater, and glacially carved mountains and valleys (Boggs et al. 2008). The study area encompasses the shoreline portions of Glacier Bay, Gulf of Alaska, Icy Strait, the mouth of the glacial-fed Alsek River, and areas surrounding the Chilkat and Fairweather Mountain Ranges. The majority of the alpine zone in the northern and western portions of the study area remains covered in ice fields. Resident human population in the area is sparse and restricted to a single town (Gustavus, population ~400) including the National Park headquarters along the southern boundary of the Park. The rest of the study area is essentially devoid of human development. While the shoreline of Glacier Bay receives a limited amount of human recreational use in summer (750-1500 backcountry visitors annually) the marine waters of Glacier Bay receive over 400,000 visitors via motorized vessel, mainly cruise ships. (NPS unpublished data). Access to the Park is by airplane or boat.

Successional chronosequences vary substantially in rate and character within the study, but generally follows this path in low elevation sites: pioneer communities of algae/lichen, seral forbs, and *Dryas drummondii* in areas glaciated within 50 ybp; open and closed scrub from 50-100 ybp; young forests from 100-300 ybp; and a mature community mosaic of old growth forests with *Sphagnum* muskegs in areas that remained ice-free during the LIA (Chapin et al. 1994). Early pioneer stage plants offer few food resources to bears, but open scrub habitats often contain a mosaic of bear foods including soapberry, strawberry (*Fragaria chiloensis*), locoweed, and bear root in the northwest portion of Glacier Bay. Closed scrub habitats dominated by willow (*Salix* spp.) often contain extensive soapberry, while alder-dominated (*Alnus* spp.) closed scrub contains little high-quality bear forage with the exception of groundcone (*Boschniakia rossica*), an alder root parasite (Pojar et al. 1994). Young forests in the southern portion of the Glacier Bay are dominated by dense (>60% canopy cover) Sitka spruce (*Picea sitchensis*) with little understory. Several berry-producing species including blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and red elderberry (*Sambucus racemosa*) grow in limited abundance in young forest openings and fringe. Areas surrounding Glacier Bay that were not glaciated during the LIA consist of old-growth hemlock (*Tsuga heterophylla*) and spruce forests with interspersed peat muskegs. Old growth communities often contain dense understories of berry-producing plants including blueberry, salmonberry and devil's club berries (*Oplopanax horridus*). Skunk cabbage (*Lysichiton americanus*) is also common in wet areas. Old growth forests are open (<60% canopy cover) or closed, and support important spring sedge (*Carex* spp.) habitat. Riparian zones host seasonal anadromous fish runs that increase in diversity with number of years since glaciation (Milner et al. 2000). A large portion of the coastline throughout the area is bordered by recently uplifted graminoid and herbaceous beach meadows. Bear foods in these meadows include strawberry nagoonberry (*Rubus arctica*), dandelion (*Taraxicum* spp.), horsetail (*Equisetum* spp.), angelica (*Angelica lucida*), cow parsnip (*Heracleum lanatum*), beach lovage (*Ligusticum hutenii*), pacific hemlock-parsley (*Conioselium chinense*), and grasses. In addition to the diversity of plants available,

intertidal food sources along the shoreline include acorn barnacles (*Balanus* spp.), mussels (*Mytilus trossulus*), and rock gunnels (*Stichaedae/Pholidae*). Other potential prey species throughout the study area include moose (*Alces alces*), mountain goats (*Oreamnos americanus*), voles (*Myodes* and *Mycrotus* spp.), and ground-nesting birds.

Sampling

Sampling units were sections of shoreline selected from uplifted beach meadows at mouths of perennial streams within GLBA ranging from 0.02 to 0.55 (mean = 0.1) km^2 in size. Shoreline meadows and stream mouths have been identified as areas of importance to bears (Partridge et al. 2009) and were chosen to maximize the likelihood of black and brown bear occurrence and minimize modeling problems associated with low occupancy. In addition, the coast of Glacier Bay is logistically feasible to reach and is the primary location of bears-human interactions, so the shoreline bear distributions are most relevant to managers. Because I sampled only shoreline locations, the range of inference for this study included only shoreline stream mouths and did not extend inland. However given the large home ranges of both species, it is not realistic that bears spend their entire lives on the coast, and occurrence at shoreline sites likely indicated occurrence at adjacent inland sites. To determine these locations, I identified 78 perennial watersheds (including glaciers) that were logistically feasible to visit and used Streveler (1996), Geiselman et al. (1997), and Milner et al. (2000) to establish the approximate dates of deglaciation at the mouths of these streams. I stratified potential sampling units into five categories based on four distinct periods of deglaciation identified in a USGS ice-extent GIS layer (Geiselman et al. 1997, Fig.1.1). The resulting strata included: pre-1750 AD (>260 ybp), 1750-1860 AD (150-260 ybp), 1860-1890 AD (120-150 ybp), 1890-1930 AD (80-120 ybp) and 1930 to present (<80 ybp). I randomly chose eight sampling units from each stratum (total n = 40; Fig. 1.2). The oldest stratum (>260 years) was surveyed only in year 2 (2010) of the study. The average nearest-neighbor distance between sampling

units was 6.5 km and each sampling unit was surveyed 2-7 times from May to September in 2009 and 2010.

I used motorized vessels to access shoreline sampling units for surveys. Bear species were detected and identified by a combination of direct observation, genetic analysis of hair, and/or identification of tracks. The field crew began each survey with a scan of the area with binoculars from the boat, and if a bear was observed at the site, we simply noted the species and refrained from further disturbance or displacement. If no bears were sighted, 2-4 observers conducted a ground survey. The amount of shoreline covered in the ground survey was determined by the terrain available for sign surveys, and total sampled area was calculated for each study site using Geographic Positioning Systems (GPS) units. Observers walked parallel transects through study areas searching for bear hair, tracks, and scat using methods outlined in Partridge et al. (2009). Hair was collected opportunistically from trails and systematically from bear rub trees that were documented with GPS units, affixed with ~ 40-cm long pieces of barbed wire to enhance hair collection for the duration of the study, and checked on every site visit. Hair samples were sent to Wildlife Genetics International (Nelson BC, Canada) where DNA was purified using QIAGEN DNeasy spin columns. Species identification of extracted samples was performed via sequences-based analysis of a portion of the mitochondrial 16S rRNA gene (Johnson and O'Brien 1996).

I determined species occurrence using tracks if I found front paw tracks with distinct indentations from the toes and claws. Black bears were identified from tracks with a curved toe arc and short front claws (<3.8 cm), while brown bears were identified with a strait toe arc and long claws (≥3.8 cm) (Herrero 1985). Bear observations, hair collection locations, tracks, and scats were recorded with a Trimble Global Positioning System handheld unit (Trimble GeoExplorer3, Trimble Navigation Limited, Sunnyvale, CA, USA) and exported into a Geographic Information System (GIS) program (ESRI ArcGIS 9.x. Redlands, CA, USA). I also collected relevant survey data during each visit including the number of observer minutes, tide height, presence of salmon, and the

number of bear scats as an index of bear activity (Partridge et al. 2009). Sampling unit covariate data collected included the number and composition of plant and intertidal bear foods (NPS 2009), the number of bear rub trees, presence of salmon, and presence of tracking substrate.

Analysis

To model occupancy, I originally examined a number of sampling-unit and survey covariates that would potentially influence detection and occurrence (Table 1.2). Landcover covariates were adapted from the NPS Inventory and Monitoring Program Landcover Map based on 1996 1:65,000 color infrared aerial imagery (Boggs et al. 2008). Forty four specific landcover classes were condensed into 17 broader categories (Fig. 1.3). I calculated the percentage of six different landcover classes within 1-km and 5-km buffers (3.1 and 78.5 km^2, respectively) around the center points of sampling units using ArcGIS (ESRI, Redlands, CA, USA) software. I also added a binary covariate of young forest (deglaciated 150-260 ybp) to specifically test for the effects of this successional stage on black and brown bear distributions. Terrain rugosity was calculated within 5-km buffers of sampling units by dividing the surface area of each grid cell by the planimetric area using source digital elevation models (DEM, NPS GIS layer) and GIS extension DEM Surface Tools v.2.1.254 (Jenness 2010). I also used GIS to calculate the area of each watershed, the proportion of each watershed glaciated, the area of each sampling unit, and the average nearest-neighbor distance between sampling units.

Presence/absence of black and brown bears as well as sampling-unit and survey covariates were entered and analyzed in program PRESENCE (Proteus Wildlife Research Consultants, Dunedin, New Zealand). To determine occupancy probability (ψ) while accounting for detection error (ρ), I attempted to generate single-species and 2-species co-occurrence single-state and-single season occupancy models using a maximum likelihood approach (MacKenzie et al. 2006). I developed a preliminary set of predictor variables for the detection and occupancy of each species (Table 1.2), and then examined correlation between variables based on Pearson correlation coefficients. I removed one

variable of each set of correlated variables (Pearson coefficient > 0.65) to maximize parsimony and model fit. I created models using each detection covariate, and then combinations of detection covariates from the top models. I then tested all variables that in top models for detection as occupancy covariates. I used Akaike Information Criterion (AIC) to determine best-fitting models (highest AIC values with difference < 2, Burnham and Anderson 2002) differences for black bears, brown bears, and co-occurrence.

Results

From May-September, field crews surveyed 32 sites in 2009 and 40 sites in 2010 (Fig. 1.2) 2-7 times each for a total of 211 surveys. The proportions of brown and black bear detections across all surveys were highest using tracks, followed by genetic analysis and then direct observation (Table 1.3a). The proportion of detections per sampling unit for all methods combined was consistent for both species between 2009 and 2010 while the proportion of detections per survey increased slightly for both species in 2010 (Table 1.3b). Black bears and brown bears were detected together in 19.0% of the surveys (40/211). Total naïve occupancy estimates (percentage of sampling units in which species was detected at least once) across all 40 sites for both years were 100% (40/40 sites) for brown bears, and 52.5% (21/40 sites) for black bears (Table 1.3b, Fig. 1.4). The mean proportions of detections per sampling unit were significantly higher in recently glaciated and old-forest units than in young-forest units for brown bears, and significantly lower in recently glaciated units than young- and old-forest units for black bears (Fig.1.5).

The six landcover classes within 5-km buffers were correlated with the corresponding landcover classes within 1-km buffers (r > 0.65), so I eliminated the 5-km landcover covariates. After removing the remaining correlated variables, the final set of covariates included six survey-specific variables and 11 site-specific variables (Table 1.4). These variables were used to test the fit of 27 models for brown bears and 36 models for black bears. Because brown bears were detected at all sites, I could not test

occupancy covariates for brown bears or co-occurrence models for both species. Tracks, SiteSize, OS1km, Yforest, Year, and Time appeared in top brown bear models (ΔAIC < 2) as detection covariates with occupancy fixed at 1 (Table 1.5). Coefficients indicate that presence of Tracks (β = 0.78), SiteSize (β = 0.78), OS1km (β = 0.62), were positive predictors of brown bear detectability, while Yforest (β = -0.23), Year (β = -0.23), and Time (β = -0.68), were negative predictors (Table 1.6). For black bears, CF1km was an important occupancy covariate and Rubs an important detection covariate in the top eight models with delta AIC < 2 (Table 1.5). Coefficients indicate that CF1km was a strong positive predictor of occurrence (β = 1), and Rubs were a positive predictor of detection (β = 0.61, Table 1.6). Black bears were not detected at any sites where CF1km = 0, and were detected at 21 of 24 sites (0.88) with any proportion of closed forest.

Discussion

Results of this study indicate that brown bears occupy all of the shoreline stream mouths of Glacier Bay and that the probability of occurrence of black bears was closely correlated with closed forest. Brown bears were detected in higher proportions in recently glaciated and old-growth forest than young-forest units while black bears were detected in higher proportions in young and old forest than recently glaciated units. Detection probabilities of black bears were not lower in the presence of brown bears. The results of this study do not provide evidence that black bear competition is limiting the range expansion of brown bears, or vice versa, for the following reasons: 1) brown bears occurred at all sites, 2) black bear presence was closely related to closed forest, and 3) detection of one species did not affect the detection of the other.

Brown bear models

Occupancy models for brown bears could not be generated because this species was detected at least once in every sampling unit, indicating 100% occupancy of the units. Given the large and variable home range sizes of brown bears (24-8171 km^2, McLoughlin et al. 1999) and small areas of the sampling units (mean 0.10 km^2), occupancy closure assumptions were violated. Bears undoubtedly moved in and out of study sites over the

two year "season". Therefore, detection of a species was dependent on two conditions: 1) the species was present in the study site, and 2) it was detected (MacKenzie et al. 2006). Assuming that the total population size in the study area did not change over the course of the study, and that individual movements in and out of the study sites were random with regard to timing of surveys, detection at a given site can be viewed as a surrogate for use of that site (MacKenzie et al. 2006). The models generated for brown bears yielded predictors of detection or use as a function of environmental variables, but unfortunately, it is impossible to distinguish between the two within this model parameterization. The presence of tracking substrate (Tracks) within a sampling unit likely affected detection probabilities, not use, because tracks were the most successful detection method for brown bears (Table 1.3). Similarly, SiteSize and Time were likely predictors of detection because larger areas likely contain a higher abundance of tracks and/or hair samples available to detect, and because tracks and successful genotyping from hair samples diminish over time. Coefficients in the top brown bear model indicated that young forest (YForest) units had a negative influence on detection/use while the proportion of open scrub within 1 km (OS1km) had a positive influence on detection/use. I believe these covariates are more likely representative of brown bear use than detection because 1) these covariates did not appear to affect black bear detection, and 2) historically, a low number of documented detections and anecdotal brown bear reports have occurred in young forest areas (Partridge et al. 2009, NPS 2009), and 3) open scrub habitats are common in periglacial areas, and although highly variable in habitat quality, do contain important brown bear plant foods in high abundance in many areas (NPS 2009, Partridge et al. 2009). While this study documents brown bears present in the young forest areas of Glacier Bay, these results could indicate higher use in recently glaciated and old growth than young forest habitats (Fig. 1.5).

The best brown bear model indicates that Year was a predictor of either detection or use of sampling units by brown bears. Brown bear detections per survey increased from 2009-2010 from 0.706 to 0.859 (Table 1.3b). These results could be a function of detection if observers improved their detection abilities, or it could represent an increase

in use of the study areas by brown bears in 2010 (year two). Increasing use by brown bears in areas of southern Glacier Bay is corroborated by other documented and anecdotal evidence. For example, several reports from the 1980s indicated high concentrations of black bears in Sandy and Spokane Coves, especially in the spring and early summer (Sharman and Kristensen 1982, Sharman and Coghill1982, Sharman and Brown 1983, Publicover 1985, Blackie 1989). The NPS has closed this area to camping for much of the summer for the past 20 years to minimize disturbance to bears and the potential for bear-human conflicts in an area with such high black bear densities (NPS 2009). In 2005 Partridge et al. (2009) conducted a census of bears in the Sandy/Spokane Cove area (young forest) on repeat visits using non-invasive hair collection techniques, and identified eight individual black bears and no brown bears using the area. By contrast, in from 2009-2010 we identified a minimum of four individual brown bears in the Sandy/Spokane Cove area (T. Lewis unpublished data). During the summer of 2010, brown bears were observed repeatedly in Bartlett Cove, Gustavus, and other portions of southern Glacier Bay for the first time since homesteaders exterminated brown bears over 50 years ago (NPS 2010). This trend continued in 2011 with increased encounters with brown bears in these same areas (NPS 2011). Based on previous and current study results and anecdotal sightings, it is likely that the current study occurred during a very recent range expansion by this species.

Black bear models

The probability of detecting black bears with tracks was slightly higher than genetic analysis of hair (Table 1.3a), although the number of rub trees from which hair was collected was still important for the detection of black bears. Tracks, Tide, Scats, Time, and Year also appear as detection covariates in addition to Rubs in the top black bear models indicating multiple variables influencing detection. Black bear distribution was not random across the landscape because site occupancy was very highly associated with closed forest within 1 km. Black bears have long been regarded as strongly associated with forest habitats (Hall 1981). Long et al. (2010) found site occupancy by black bears in Vermont was positively associated with percent forest and negatively associated with

percent human development. Wooding and Ward (1997) provide evidence that for at least 18,000 years, the biogeography of black bears across North America has been tightly linked with historic forest habitat availability, including forest refugia during the last glacial maximum. While closed forest was an excellent predictor of black bear presence, the binary covariate Yforest was not a good predictor. Black bears were present in all of the young forest units (glaciated 150-260 ybp), as well as six of eight (75%) old forest sites, and seven of 16 (44%) sites deglaciated 80-150 ybp, refuting predictions that they would be present only in young forests. I did not detect black bears sites deglaciated <80 ybp, which were still unforested. The close association between black bears and closed forest found in this study suggests that black bears will likely expand their range northward as plant communities mature and forest develops. While the range of inference for this study only includes the shoreline areas specifically at the mouths of perennial watershed and does not extend to inland locations, it is known that black bears utilize inland forested habitats as well. The Alaska Department of Fish and Game (AFD&G) estimates that black bear densities in northern Southeast Alaska to be 1.5 bears/forested mi^2 (0.57 bears/forested km^2) based on studies in similar terrain in Washington (Barten 2005 a and b). Given this density estimate and the estimated area of closed forest in GLBA (1042 km^2, calculated from Boggs et al. 2008), an estimated 594 black bears occupy GLBA's closed forests. Use of other inland habitats by black bears has been documented near Glacier Bay. For example, during a single four hour aerial mountain goat survey over the Chilkat Mountains in Sept. 2006, ADF&G biologists counted 105 black bears in the alpine zone (Barten 2006).

Species interaction

The results of this study indicate that black and brown bear distributions overlap much more than previously believed. Two-species co-occurrence models were not feasible because brown bears occupied 100% of the sites. However, the top brown bear model did not indicate that black bear occurrence or detection affected brown bear detection/use. Similarly, the top black bear models did not indicate that brown bear detection affected black bear detection. Both species were detected in the same surveys

19.0% of the time, indicating that while dietary and temporal segregation may be occurring, the two species recurrently occupy the same locations. Mattson et al. (2005) presented evidence that exploitation competition with black bears may reduce brown bear reproduction and recruitment to the point of inhibiting range expansion across regions of North America with robust black bear populations. They suggested that the mutually exclusive distribution of brown and black bears on the coastal islands of the Pacific Northwest was caused by the combination of limited female brown bear dispersal capabilities across marine fjords (Paetkau et al. 1998) and competition with black bears. They postulated that black bears, with 8-11 fold higher densities, have the capability of foraging more intensively where sympatric with brown bears, particularly in areas with dispersed or limited food resources, e.g., without abundant root foods, spawning salmon, ungulates. While the majority of forage species of bears in Glacier Bay appears to be forb and berry species (Partridge et al. 2009), roots, spawning salmon, ungulates are also present. Similar to Partridge et al. 2009, I found that species richness (the number of possible bear foods present at site) was lowest in recently glaciated areas and highest in forested areas based on (Fig. 1.6). While bear food diversity may increase as vegetative and stream communities mature, this may not represent a direct increase in biomass. Shoreline sites in the young forest may contain a higher diversity of bear foods, but certain periglacial habitats such as low open scrub contain high quality forage species, including roots which brown bears target. Scrub habitats contain the highest coverage of locoweed and bear root, two plant foods heavily grazed and excavated in northern Glacier Bay study sites (Partridge et al. 2009). The abundant root source and lack of forest in recently glaciated areas may create a niche for brown bears to escape potential interspecific competition.

Mowat and Heard (2006) analyzed bear diets in Glacier Bay using stable isotope analysis to assess the proportion of assimilated carbon and nitrogen coming from plant, marine, and terrestrial meat sources. Their results indicated a diet composed of 69% plant, 31% marine, and 0% terrestrial meat sources. The proportion of marine-derived food sources found in the diets of Glacier Bay brown bears was low compared to diets of

brown bears along the coastline of British Columbia and elsewhere in Alaska (Mowat and Heard 2006) indicating brown bears in Glacier Bay do not have access to as much salmon as other coastal populations. During this study I observed spawning salmon in 22 out of 40 sampling units, including 13 out of 16 units glaciated >150 ybp. The number of anadromous streams will continue to increase as the riparian zones continue to mature (Milner et al. 2000). Similarly, ungulate abundance in southern Glacier Bay has increased since the 1980s as moose numbers have colonized the area. A population irruption led to a peak density of 3.9 moose/km^2 in the southern Glacier Bay/Gustavus area in 2003 (White et al. 2007) that has since declined (ADF&G unpublished data). Increased numbers of moose in southern Glacier Bay maximizes both scavenging and the prey base for bears, and creates an advantage for brown bears in resource defense competition (Mattson et al. 2005).

Because salmon resources, ungulates, and roots are present, black bears are unlikely to out-compete brown bears through exploitation competition, but brown bears may be able to outcompete black bears temporally in resource defense competition. While resource defense competition and dietary and/or temporal segregation may be occurring between brown and black bears in Glacier Bay, this study provides no evidence that either species limits the range of the other given 100% occupancy by brown bears and black bears' close association with closed forest which provides a clear explanation of their distribution.

Brown bear range expansion/recolonization

The results of this study are consistent with anecdotal evidence that brown bears have increased their range to include the southern portion of Glacier Bay. However, every documented sighting and detection during this study indicated the presence of single brown bears, not family groups. Male brown bears are capable of dispersing distances up to 60-70 km from their natal range (Rogers 1987, Blanchard and Knight 1991), which is almost three-quarters of the length of Glacier Bay. Recolonization of Glacier Bay by males could take place over as little as a single generation, although without females to

mate with true range expansion will not occur. True colonization likely takes considerably longer due to the low dispersal rates of females and long generation time. Genetic analysis of brown bears detected in the young-forest sites shows a male bias of 2(n=8) to 1(n=4) (T. Lewis unpublished data). It is possible that an unprecedented high level of recruitment of brown bears in surrounding areas over the last 5-10 years has led to increased immigration into new areas, particularly by subadult and adult males who tend to disperse the greatest distance (Blanchard and Knight 1991, Mattson et al. 2005). While competition with black bears does not initially appear to be affecting immigration of individual brown bears, successful reproduction and recruitment will be necessary to determine the longevity of this species range expansion in Glacier Bay.

A distinct advantage that brown bears have in recolonizing southern Glacier Bay after the LIA is that they can do so without crossing marine waters by immigrating from both the east and the west. In addition, food resources such as roots, salmon, and ungulates are available to brown bears throughout the area, giving them a distinct advantage in resource defense competition. If the young forest habitats of southern Glacier Bay are adequate for brown bears, dispersal into the area is feasible, and competition with black bears is not detrimental to reproduction and recruitment, why haven't brown bears recolonized sooner? While brown bears were likely extirpated from Gustavus by the homesteaders over 50 years ago, Glacier Bay National Park has been closed to hunting for over 80 years, providing ample habitat for brown bears in southern Glacier Bay. It is possible, but not likely, that brown bears were present but not observed in these areas of the park for the past 50 years. It is also possible that recolonization of Glacier Bay by brown bears after the LIA is occurring from the north, and the southern portion of the bay is at the tail end of this post-glacial recovery. The coast is believed to be an important travel corridor for black and brown bears, but Streveler and Smith (1987) described two other potential immigration corridors into Glacier Bay: the Tarr Inlet–Melbern Glacier corridor in the upper west arm, and the Goddess River–Endicott River, otherwise known as the Endicott Gap, in the lower east arm (Fig. 1.7). They proposed that the Endicott Gap corridor has played a large role in the establishment of mammals,

including brown and black bears, in upper Glacier Bay. It is possible that with slow dispersal of females through these northern corridors, brown bears are just now re-colonizing southern Glacier Bay. This scenario, however, would not explain the presence of brown bears in Gustavus 50 years ago. Another possible explanation is that there have been two distinct waves of colonization, the first over 50 years ago in which brown bears moved into Gustavus, and the second occurring presently. If this is the case, why was the first colonization wave unsuccessful? The young forest habitat was likely less developed 50 years ago so it is possible that a combination of marginal habitat, harvest pressure from Gustavus, and possibly exploitation competition with black bears prevented brown bears from successfully expanding their range at that time.

Management implications

In the coastal Glacier Bay region, brown bears not only occupy recently glaciated and old growth landscapes, but also occupy young forest regions, although frequency of use of those habitats may be lower. The success of this apparent range expansion is yet to be determined. The probability of occurrence of black bears is closely related to closed forest. Managers can expect that as the landscape of northern Glacier Bay matures from open and closed scrub into young forest, brown bears will still be present but their use of these areas may decrease, and black bears will expand their range northward.

From 2010-2011 anecdotal and documented reports indicate that brown bears have increased their range to include the GLBA headquarters and the adjacent town of Gustavus. The results from this study corroborate these reports and provide evidence that this range expansion extends throughout the southern forested portion of Glacier Bay. Range expansion for grizzly/brown bears has been documented in the Yellowstone and Northern Continental Divide populations (Bader 2000) after near extirpation in the 1800s through mid-1900s (Mattson and Merrill 2002). Continued success in recovery of these populations is likely dependent on controlling human development/habitat fragmentation, and tolerance of bears by humans (Pyare et al. 2004). In the Glacier Bay ecosystem,

anthropogenic habitat fragmentation is unlikely to affect range expansion due to the level of protection of the National Park (large tracts of Wilderness, no hunting, etc.). Human tolerance, however, will be important for permanent range expansion of brown bears on the Gustavus forelands, an area of private land surrounded by park lands. Benn and Herrero (2002) analyzed 119 records from 1971-1998 of human-caused grizzly bear mortalities in Banff and Yoho National Parks in Canada and found that control of "nuisance" bears accounted for 71% of these deaths respectively and that adult females and dependant young accounted for 65% of the total human caused mortality. The authors attribute the large proportion of management destructions of females with cubs to their likelihood to habituate to humans, obtain access to human food and attractants, and become a nuisance. Suring and Del Frate (2002) found that defense of life and property (DLP) kills of brown bears on the Kenai Peninsula, Alaska, were most common in rural areas near residences and roads. Wilder (2003) found subadult males made up the majority of bears killed in DLP from 2000-2001 (n=8) on private lands adjacent to Wrangell St. Elias National Park, and proposed that this area constituted a population sink for dispersing bears. Human-caused mortality of brown bears in Gustavus could similarly serve as a dispersal sink and limit effective range expansion but would not likely affect the overall Glacier Bay population. During the course of this study, one subadult male brown bear was illegally shot in the center of the town of Gustavus (NPS 2010). Educating and helping residents to secure bear attractants and be tolerant of brown bears in Gustavus to prevent DLP kills could minimize this effect.

Although there is evidence that brown bear use is less frequent in these newly recolonized areas, the potential for humans to encounter brown bears is greater than previously believed, and educational and management actions to minimize bear-human conflicts are warranted. Brown bears are considered more dangerous than black bears because of their behavioral trait of attacking when surprised or threatened (Herrero 1985). Educating residents and visitors about ways to avoid (e.g., make noise when traveling through thick brush) and how to respond (e.g., talk calmly) during a surprise encounter can minimize the potential for harm to both people and bears.

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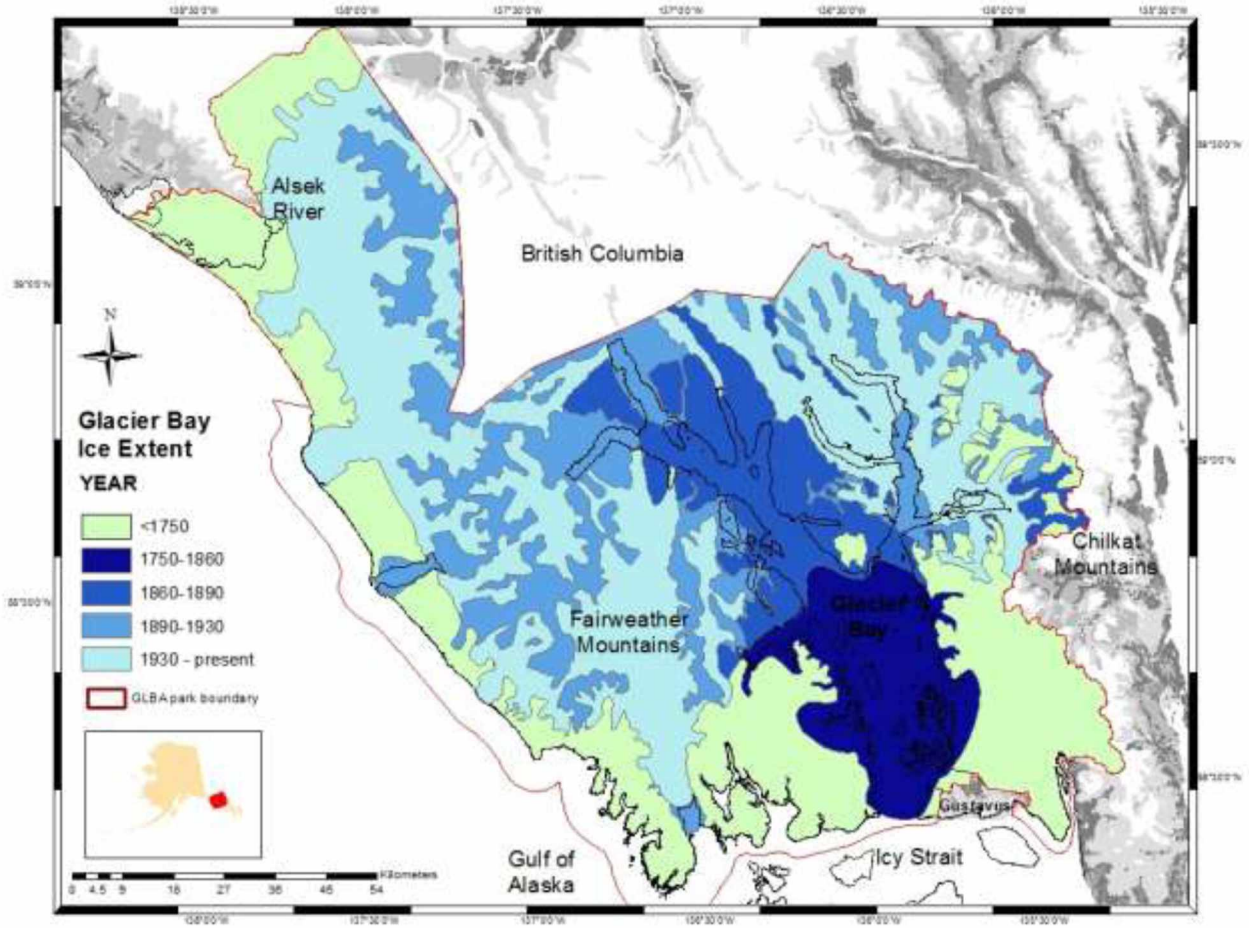

Fig 1.1. Ice extent and retreat by year in Glacier Bay National Park and Preserve (GLBA), Alaska since the Little Ice Age. Land colored green within the GLBA boundary was not glaciated since the end the last glacial maximum (~10-12,000 ybp).

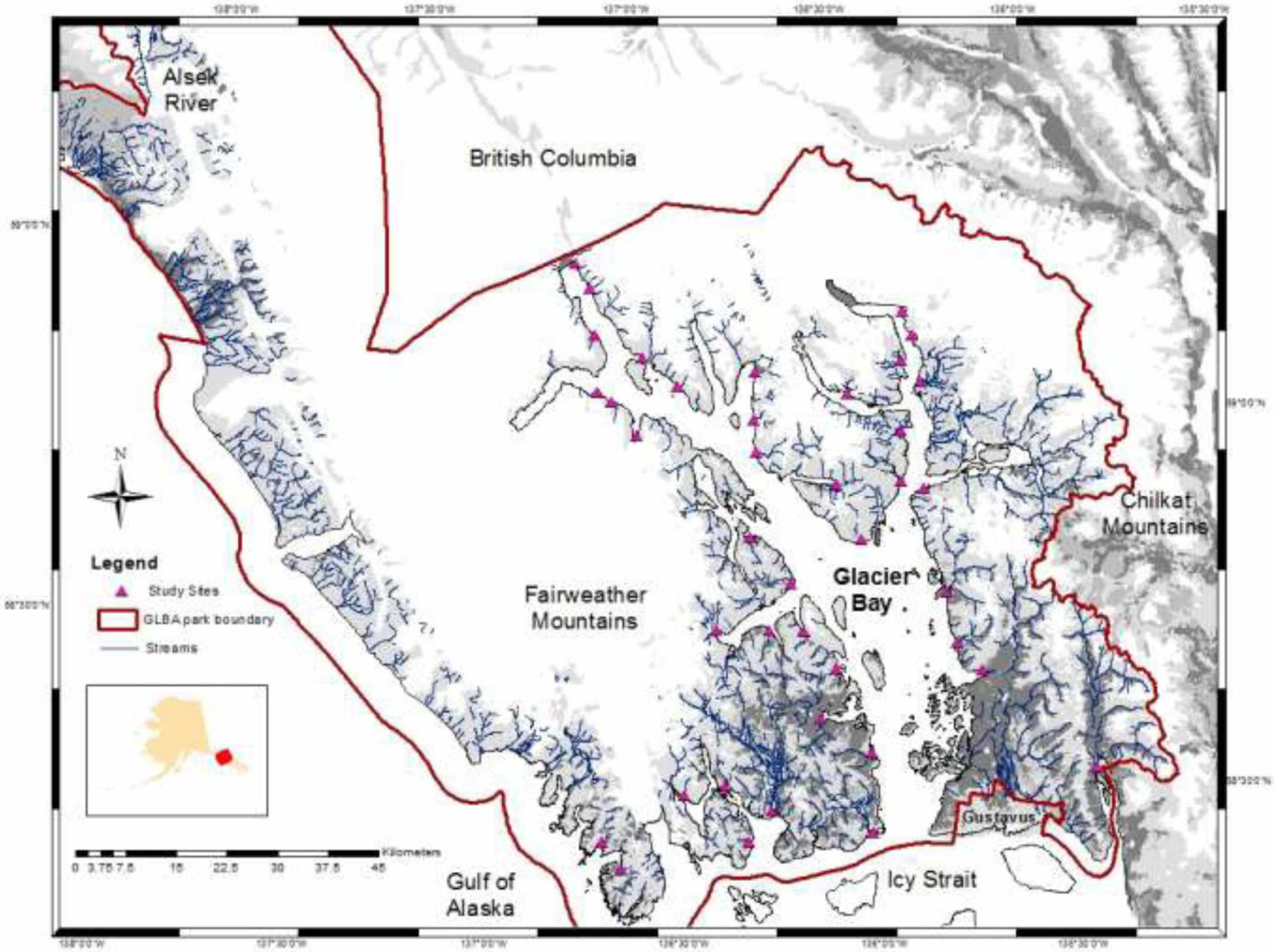

Fig 1.2. Location of study area and sampling locations for black and brown bear surveys in 40 sites in GLBA, 2009-2010.

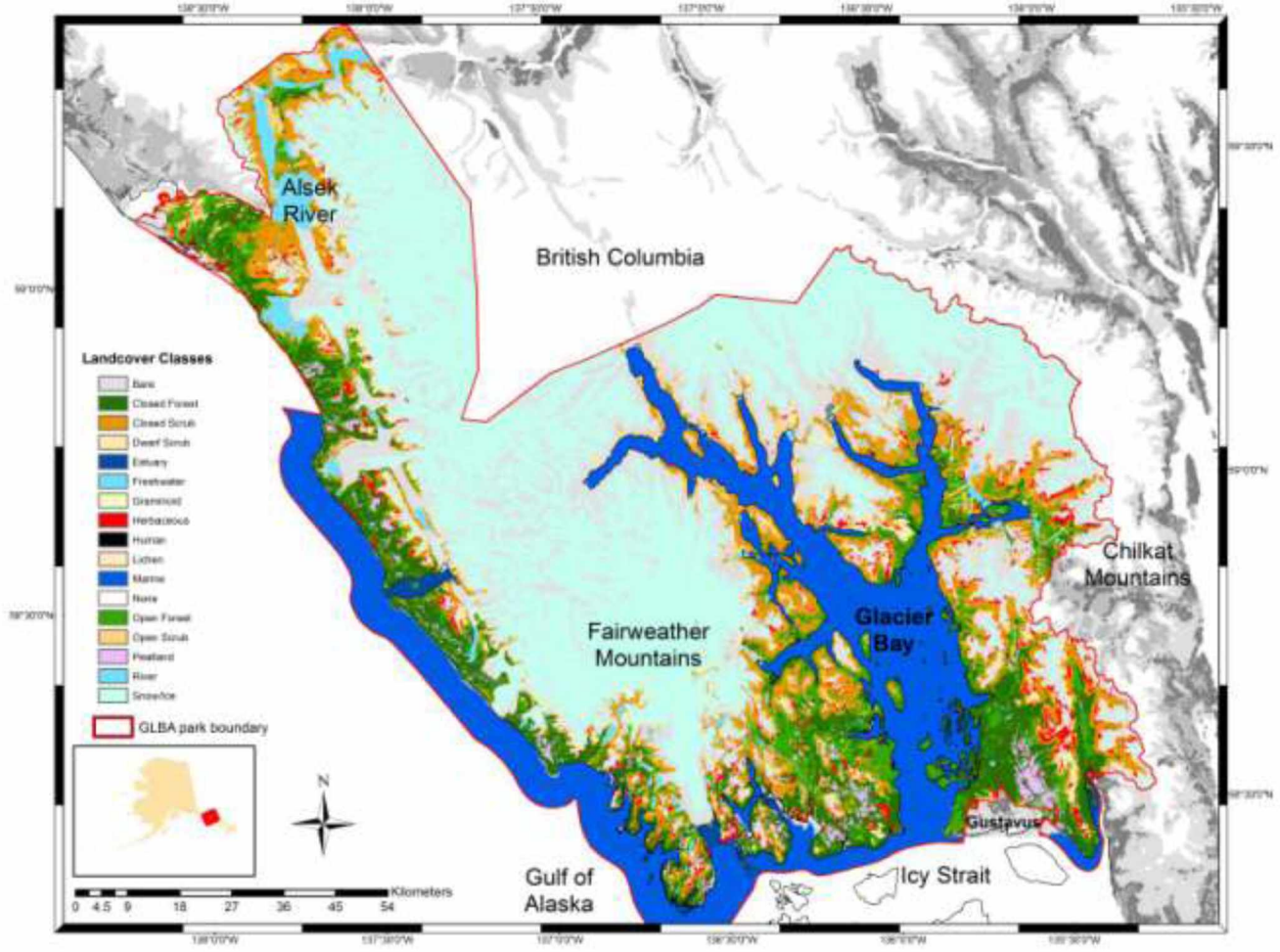

Fig 1.3. Landcover classes examined as covariates in this brown and black bear distribution study, 2009-2010. Classes were adapted from NPS Inventory and Monitoring Landcover Map (Boggs et al. 2008).

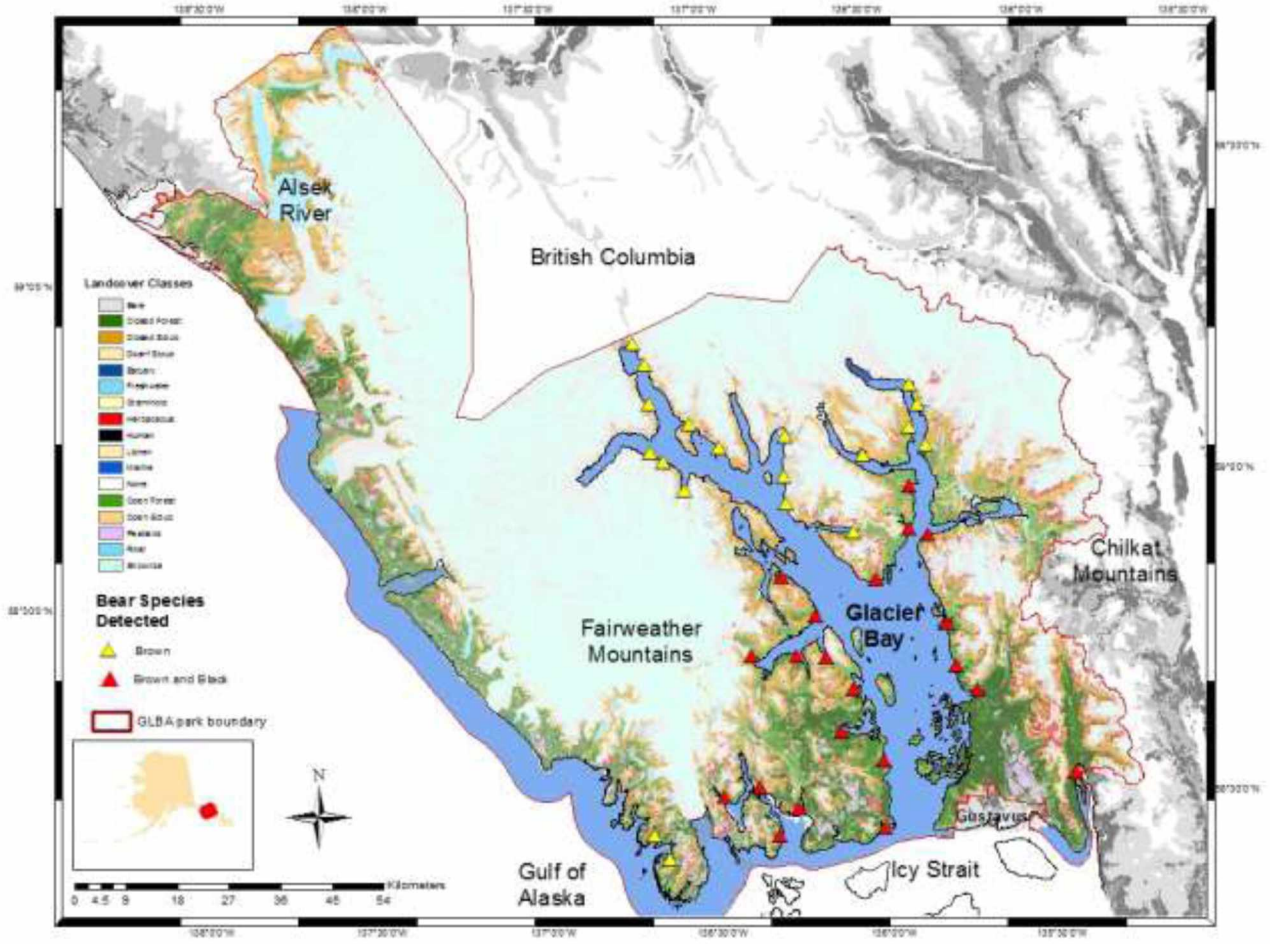

Fig. 1.4. Detection patterns of black and brown bears in sampling locations in GLBA, 2009-2010. Brown bears were detected in all 40 of the sites, and black bears were detected in 21 sites.

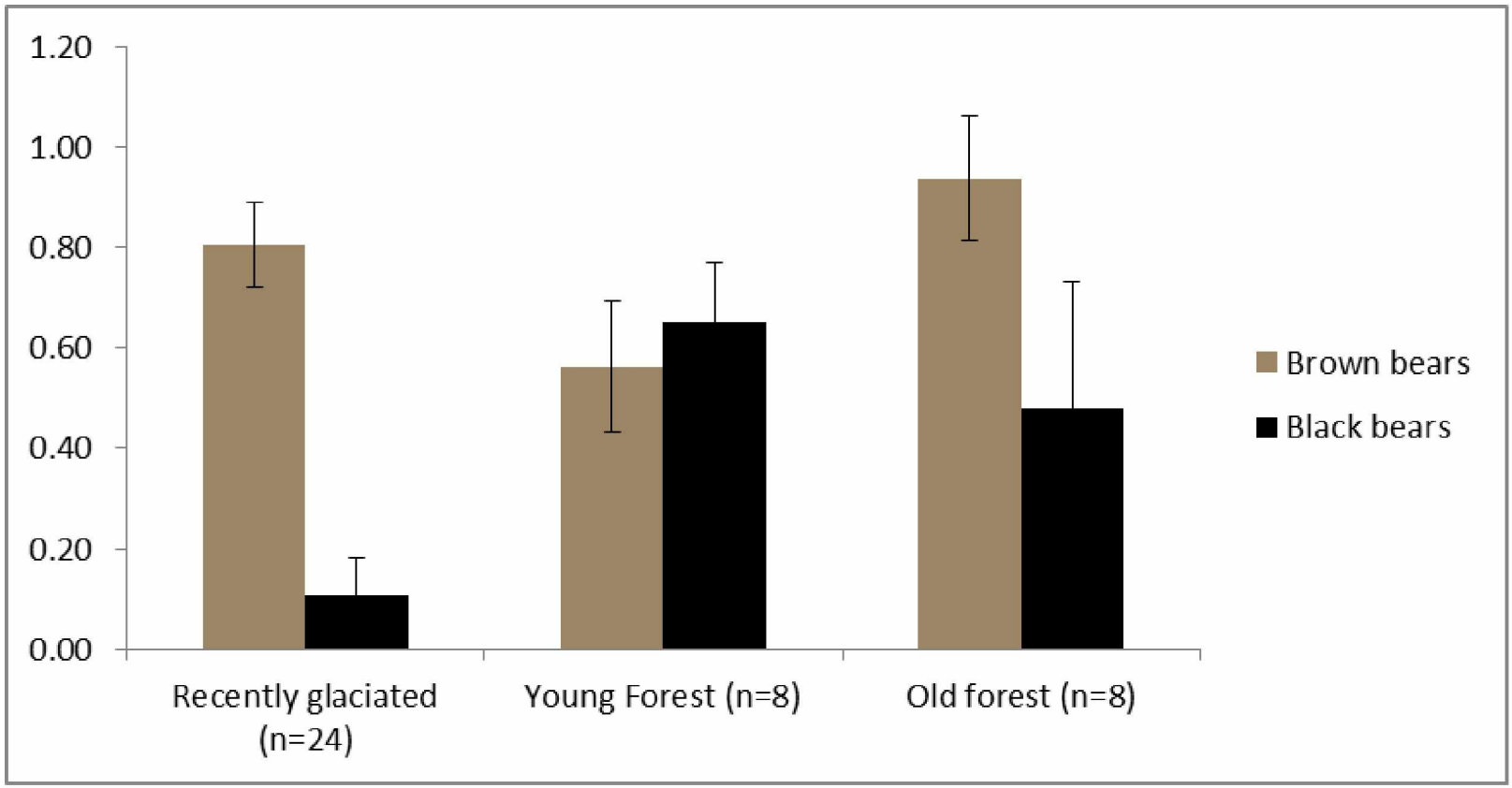

Fig 1.5. Mean proportion of detections per sampling unit of black and brown bears in recently glaciated (<150 ybp), young forest (150-260 ybp) and old forest (>260 ybp) across 40 sampling units in GLBA. Error bars represent 95% confidence intervals.

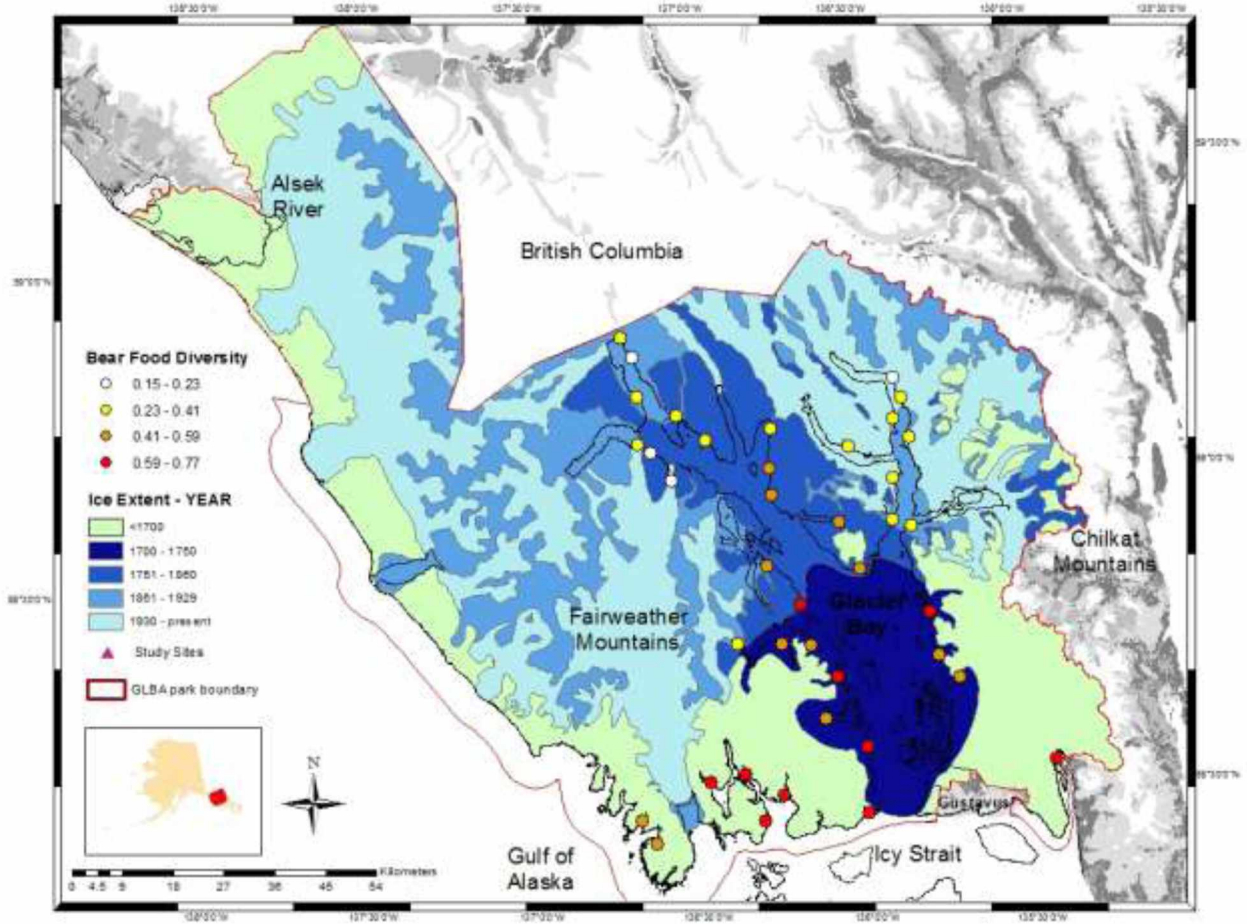

Fig. 1.6. Bear food species diversity at 40 study sites in relation to time since deglaciation in GLBA, 2009-2010. Diversity equals the number of foods at site/number in study area. Land colored grey within the GLBA boundary was not glaciated since the end the last glacial maximum (~12,000 ybp).

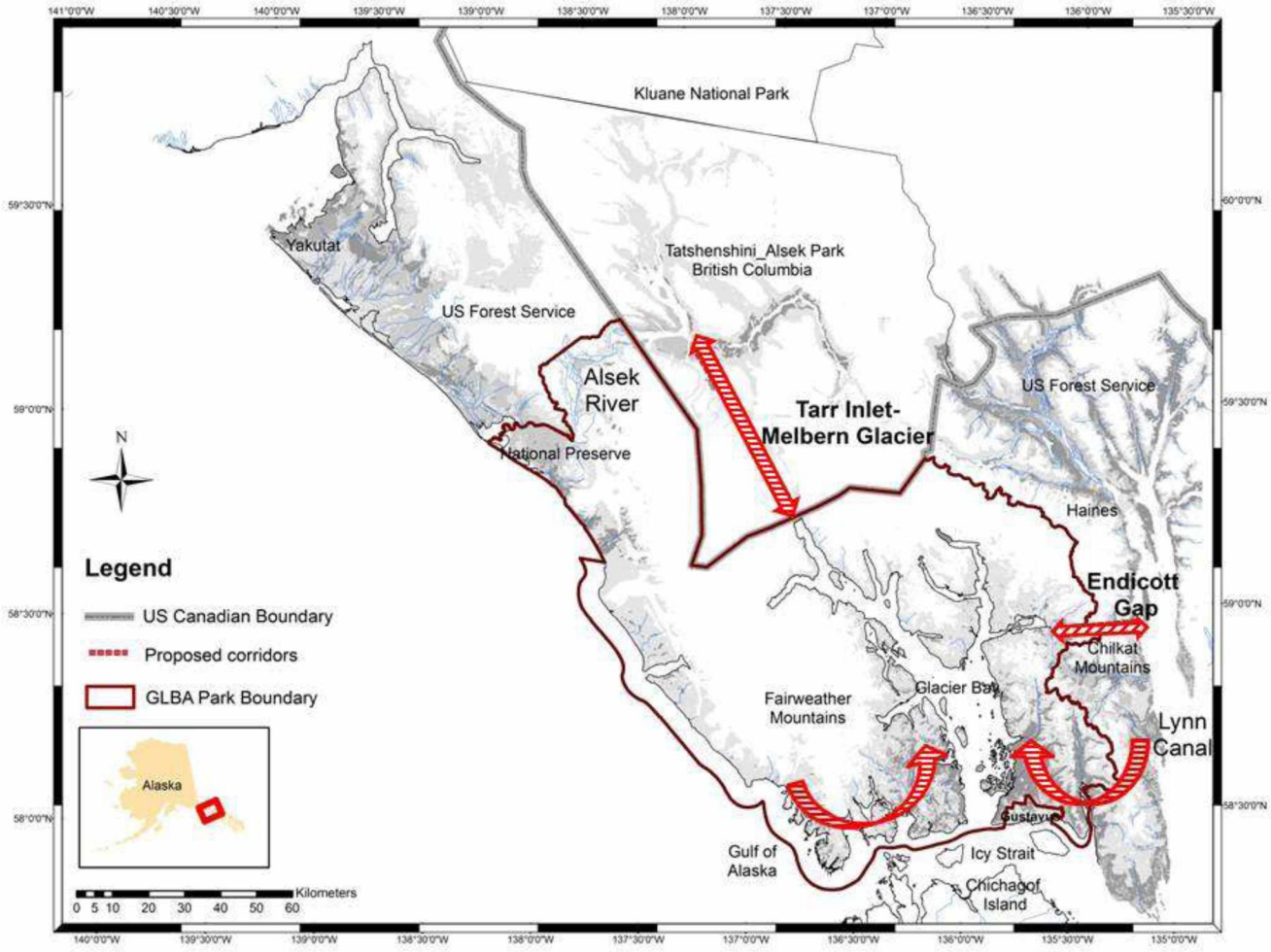

Fig. 1.7. Proposed migration corridors for black and brown bears in GLBA.

Table 1.1. Demographic and life history traits of black and brown bears.

Life history trait	Black bears	Brown bears	Sources
Mean density across western North America	16.4 bears/100 km^2	2.2 bears/100 km^2	Mattson et al. 2005
Female mean home range size across western North America	63 km^2	321 km^2	Mattson et al. 2005
Mean male dispersal ranges	13.4 – 61 km	41.9 – 70 km	Lee and Vaughan 2003 Rogers 1987 Proctor et al. 2004 Blanchard and Knight 1991
Mean age of first reproduction across Western North America	6.2	6.1	Mattson et al. 2005
Mean litter interval across Western North America	2.4	3.0	Mattson et al. 2005

Table 1.2. Initial covariates considered for bear occupancy models, Glacier Bay 2009-2010.

Covariate	Unit	Method/Source	Justification
Effort	Observer minutes/area of sampling unit	Recorded on site	To standardize effort across surveys
Tide	1 (low tide) or 0 (not low tide)	Low tide < 0 tide height in tide book	Detection by observation or tracks potentially higher at low tide
Scats	Number of scats observed per survey	Recorded with GPS	Index of bear activity (Partridge et al. 2009)
Year	1 (2009) or 0 (2010)	Recorded	To account for possible differences in detection between years
Time	Number of days since last visit	Calculated	Tracks and quality of hair samples diminish over time
Tracks	1 (tracking substrate present) or 0 (not)	Recorded for each sample unit	Tracking substrate is necessary for detection by tracks
Rubs	Number of rub trees in sampling unit	Recorded with GPS	Number of rub trees likely influences detection by hair
Rugg	Ratio of surface to planimetric area within 5 km buffer	DEM Surface Tools (Jenness 2010)	May affect detection and occupancy
Blac/Brow	1 (other species detected) or 0 (not)	Recorded	One species affect detection and occurrence of the other
WtshSize	Area of watershed in m^2	NPS watershed GIS layer	May affect occurrence
SiteSize	Area of sampling unit in m^2	Calculated in GIS from GPS points	May affect detection
%WtshGlac	Proportion of watershed glaciated	NPS watershed and ice GIS layers	May affect occurrence
Years	Number of years since deglaciation	Streveler (1996), Geiselman et al. (1997), and Milner et al. (2000)	May affect occurrence

Table 1.2 continued.

Covariate	Unit
Foods	Number of available bear foods per unit/total number in all units
Salmon	1 (salmon in stream) or 0 (not)
Open forest	% within 1 km and 5 km buffers
Closed forest	% within 1 km and 5 km buffers
Conifer	% within 1 km and 5 km buffers
Deciduous	% within 1 km and 5 km buffers
Open scrub	% within 1 km and 5 km buffers
Herbaceous	% within 1 km and 5 km buffers
Yforest	1 (sampling unit in young forest) or 0 (not)

Method/Source	Justification
Recorded and calculated for each unit based on bear food list (NPS 2009).	Food diversity may affect occurrence
Observations	May affect occurrence
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Calculated in GIS (Boggs et al. 2008)	May affect detection and occupancy
Geiselman et al. (1997)	May affect occurrence

Table 1.3. Mean proportions of detections by sampling units with standard errors (SE) by species and method (a) and proportions of detections per sampling unit and survey by year and species across all methods (b).

a)

Method	Observation	SE	Tracks	SE	Genetic	SE	ALL	SE
Brown	0.094	0.024	0.611	0.050	0.474	0.057	0.783	0.037
Black	0.057	0.022	0.186	0.043	0.148	0.038	0.290	0.051

b)

Proportion and number (in parentheses) of detection per sampling unit by year and combined.

	2009 (n=32)	2010 (n=40)	combined (n=40)
Brown	0.969 (31)	0.925 (37)	1.000 (40)
Black	0.469 (15)	0.450 (18)	0.525 (21)

Proportion and number (in parentheses) of detections per survey by year and combined.

	2009 (n=126)	2010 (n=85)	combined (n=211)
Brown	0.706 (89)	0.859 (73)	0.768 (162)
Black	0.230	0.329	0.270 (57)

Table 1.4. Description of final variables tested for predicting black and brown bear detection and occurrence.

Covariate	Description
Tide	Binary variable, 1 = low tide during survey.
Effort	Observer minutes/area of site.
Scat	Number of scats as relative index of bear activity.
Year	Binary variable, 1 = 2009.
Time	Number of days since last survey. 365 used as value for first survey of a given study site.
Black/Brow	Binary variable representing detection of other bear species.
Rubs	Number of bear mark trees within survey area.
Tracks	Binary variable, 1 = tracking substrate present at study site.
Rugg	Average ratio of surface area to planimetric area within 5 km buffer, not including marine waters.
WtshSize	Area of watershed.
SiteSize	Area of study site.
Yforest	Binary variable, 1 = land deglaciated 150-260 ybp.
Salmon	Binary variable, 1 = salmon seasonally present in stream.
CF1km	Percent of closed forest within 1 km buffer around center of site (3.1 km^2).
OF1km	Percent of open forest within 1 km buffer around center of site (3.1 km^2).
He1km	Percent of herbaceous vegetation within 1 km buffer around center of site (3.1 km^2).
OS1km	Percent of open scrub within 1 km buffer around center of site (3.1 km^2).

Table 1.5. Results of AIC model selection of probability of detection brown bears and detection (ρ) and occurrence (ψ) of black bears in GLBA, 2009-2010.

Model	AIC	Delta AIC	No. Par.	-2*Log(L)
Brown Bear				
ψ (1), ρ (Tracks + SiteSize + OS1km – Yforest – Year – Time)	188.53	0	8	172.53
ψ (1), ρ (Tracks + SiteSize + OS1km – Yforest – Year – Time – Effort)	190.38	1.85	9	172.38
ψ (1), ρ (Tracks + SiteSize + OS1km – Yforest – Year – Time – Effort – He1km)	192.37	3.84	10	172.37
Black Bear				
ψ (CF1km), ρ (Rubs)	161.89	0	4	153.89
ψ (CF1km), ρ (Rubs – Tracks)	161.93	0.04	5	151.93
ψ (CF1km), ρ (Rubs + Tide)	162.66	0.77	5	152.66
ψ (CF1km), ρ (Rubs + Tide – Tracks)	162.85	0.96	6	150.85
ψ (CF1km), ρ (Rubs + Scats)	162.87	0.98	5	152.87
ψ (CF1km), ρ (Rubs + Time)	162.94	1.05	5	152.94
ψ (CF1km), ρ (Rubs - Year)	163.69	1.80	5	153.69
ψ (CF1km + OF1km), ρ (Rubs)	163.89	2.00	5	153.89

Included are top models for each species with Akaike value, delta AIC, number of parameters in model, and -2 log-likelihood.

Table 1.6. Untransformed and transformed estimates of coefficients (β) with standard errors (SE) for covariates in top brown and black bear occupancy/detection models.

Covariate	β log odds	β transformed	SE log odds	SE transformed
Brown bear				
constant	27.036	1	116278.668	1
Tracks	1.293	0.785	0.515	0.626
SiteSize	1.072	0.775	0.544	0.633
OS1km	0.470	0.615	0.253	0.563
Yforest	-1.202	-0.231	0.444	0.609
Year	-1.196	-0.232	0.442	0.609
Time	-0.767	-0.683	0.195	0.549
Black bear				
constant	457.571	1	45747.657	1
CF1km	584.816	1	46484.765	1
constant	-0.091	-0.477	0.193	0.458
Rubs	0.450	0.611	0.197	0.549

Chapter 2: Population and landscape genetics of brown bears in Glacier Bay, Alaska

Abstract

Southeast Alaska has a long, complex history of advancing and retreating glaciers and changing sea level throughout the Pleistocene and into the Holocene. The Little Ice Age (LIA) covered Glacier Bay in ice until approximately 260 years ago when rapid retreat began exposing land for colonization. I used DNA microsatellites to examine population structure of 105 brown bears in relation to landscape variables to determine where genetic mixing and barriers occur and determine likely population sources of brown bear recolonization of Glacier Bay. Results indicate that the shoreline of Glacier Bay hosts brown bears from three distinct populations. The ranges of two of these populations (East and West) extend well into non-park lands to the Northeast and Northwest, while the range of the third population (Glacier Bay, or GLBA) is specific to the park. The three genetic groups overlap in northern Glacier Bay although the extent of admixture between the groups is relatively low, indicating recent immigration. The GLBA group is likely composed of the original colonizers that were isolated long enough to undergo genetic drift. The southern portion of Glacier Bay fjord appears to be a barrier to dispersal, thus perpetuating the East/West genetic divide. The Fairweather Mountain range appears to further impede dispersal on the west side of Glacier Bay, as indicated by genetic differentiation between bears of Glacier Bay vs. Yakutat forelands. As the ice retreated from the south after the LIA, bears as well as other animals likely recolonized newly available terrain from both east and west refugia while Glacier Bay fjord inhibited movement of terrestrial species across the bay and funneled dispersal in a northward direction. At the northern end of Glacier Bay these populations came into secondary contact after several hundreds of years of separation, creating a population level biological contact zone.

Introduction

The Pacific Northwest has a long history of advancing and retreating glaciers and changing sea level throughout the Pleistocene and into the Holocene. Contemporary genetic diversity of species in the region is a combined result of evolutionary processes, glacial history, species' life history traits, source populations, and landscape characteristics. The biogeographic histories of biota in this region are complex due to colonization from northern and southern continental sources, as well as from ice-free coastal refugia, during the period of glacial retreat beginning approximately 18,000 years ago at the end of the Last Glacial Maximum (LGM; Klein 1965, Heaton et al. 1996, Cook et al. 2006, Carrara et al. 2007, Shafer et al. 2010a). Portions of northern Southeast Alaska were again glaciated during the Little Ice Age (LIA) from the 16th to 19th centuries (Larsen et al. 2005, Connor et al. 2009). These glacial cycles have had a great effect on the genetic diversity of plants and animals in this region through the influence of changes in species range on evolutionary processes such as genetic drift and selection. Glacial expansion isolated populations into refugia leading to decreased genetic diversity and increased differentiation, while the mixing of expanding populations after the ice retreat increased diversity and decreased differentiation (Hewitt 1996, Petit et al. 2003). Converging ancient lineages of several mammals in secondary contact zones have been detected in Southeast Alaska, including brown bears *Ursus arctos* (Talbot and Shields 1996, Paetkau et al. 1998), black bears *Ursus americanus* (Byun et al. 1997, Stone and Cook 2000, Peacock et al. 2007), American marten *Martes americanus* (Stone et al. 2002), and mountain goats *Oreamnos americanus* (Shafer et al. 2010a) indicating coastal, continental, and possibly cryptic refugial population sources. Northern Southeast Alaska contains a complex system of marine fjords and islands as well as extreme topography and extensive ice-covered terrain. Genetic diversity from ancient lineages can persist in such highly fragmented landscapes that minimize connectivity and thus slow or prevent colonization (Cook et al. 2006, Peacock et al. 2007). This diversity can be examined across various time scales using genetic markers that mutate at different rates. Mitochondrial DNA (mtDNA), with maternal inheritance and hence no recombination, is

often used to determine historical lineages while nuclear DNA such as microsatellites, with bi-parental inheritance and high variability, are used to determine contemporary diversity and gene flow (Paetkau et al. 1998, Waits et al. 1998, Chambers and MacAvoy 2000, Peacock et al. 2007). In fragmented landscapes that may have limited connectivity between source populations, it may be possible to detect historical lineages using more rapidly evolving microsatellites (Peacock et al. 2007). In this study I sought to gain insight on colonizing population sources by investigating the contemporary genetic diversity of post-expansion brown bears in a highly fragmented landscape surrounding a recently deglaciated Southeast Alaskan fjord.

Glacier Bay, in northern Southeast Alaska, has a dynamic glacial history since after the LGM (Fig. 2.1). Radiocarbon dating of interstadial wood shows evidence that old-growth forest occurred in many parts of Glacier Bay 5000-7000 years ago (Lawrence 1958, Connor et al. 2009). Approximately 500-300 years ago much of Glacier Bay was again covered in ice until approximately 260 years ago when the tidewater glaciers that covered Glacier Bay began retreating 15 times faster than anywhere else in the world (Lawrence 1958, Connor et al. 2009). This rapid recession exposed new fjords and land available for recolonization. Many areas surrounding Glacier Bay were not glaciated during the LIA, and likely served as glacial refugia to plant and mammal species during the most recent glaciations. The brown bear is one of the 29 terrestrial mammalian species that have recolonized parts or all of Glacier Bay since the LIA (Taylor 1984) from unknown sources. Brown bears have large home ranges (up to 8171 km2; McLoughlin et al. 1999) and strongly male-biased dispersal patterns, with females remaining within their mothers' home ranges while males disperse widely (42-70 km) outside of these natal ranges (Glenn and Miller 1980, Blanchard and Knight 1991, Swenson et al. 1998, Proctor et al. 2004, Mattson et al. 2005). While brown bears are capable of long-range dispersals, Paetkau et al. (1998) found that bodies of water $\geq$7 km wide greatly reduce male brown bear dispersal and those 2-4 km wide reduce female dispersal. Proctor et al. (2012) found that glaciated mountain ranges had a significant effect on genetic diversity of grizzly bears in southern Southeast Alaska and British

Columbia, while non-glaciated mountains did not. Similarly, glacier-covered mountains and extensive ice fields were found to separate black bears into genetically distinct groups in northern Southeast Alaska (Peacock et al. 2007) and South-central Alaska (Robinson 2007). The coast of Glacier Bay is believed to have been an important travel corridor for black and brown in order to avoid marine and glacial movement barriers as well as to access important marine and coastal food resources (Partridge et al. 2009). Streveler and Smith (1987) described two other potential immigration corridors into Glacier Bay: the Tarr Inlet – Melbern glacier corridor in the upper west arm, and the Goddess River – Endicott River (Endicott Gap), in the lower east arm (Fig.2.2). They postulate that the Endicott Gap corridor especially had played a large role in the establishment of mammals, including brown and black bears, in the Glacier Bay region. Animals presumably immigrate into Glacier Bay from the Northwest through the Tarr-Melbern and from the East through the Goddess-Endicott.

This study evaluated contemporary gene flow patterns and regional population structure of brown bears in the Glacier Bay region using population and landscape genetic techniques. Landscape genetics combines the principles of landscape ecology and population genetics to elucidate landscape features that affect animal movements and genetic connectivity (Manel et al. 2003). Continuing developments in molecular analysis techniques have greatly broadened the number and types of questions that can be answered with genetic data (DeYoung and Honeycut 2005). Similarly, recent developments in noninvasive genetic sampling from hair follicles and scat have allowed molecular analysis with little to no contact with the study animal (Waits and Paetkau 2005) While harvest samples can be collected on adjacent lands, hunting is not allowed in many National Parks, so non-invasively collected hair samples can be instrumental to genetic studies. I explored the regional population structure and gene flow of brown bears in and around Glacier Bay National Park and Preserve using DNA microsatellites from harvested animals and non-invasively collected hair samples. I examined this structure using standard population genetics techniques as well as landscape genetics techniques by creating landscape distance and resistance models and testing correlations

with genetic distance. Using this approach, my specific objectives were to: 1) identify the number and geographic range of subpopulations in the greater Glacier Bay region, 2) assess the level of admixture and migration within and between populations, 3) identify landscape features that limit or promote genetic connectivity and 4) identify probable migration routes and population sources of bears in Glacier Bay, which may provide insight to routes of historical colonization of brown bear in Glacier Bay following the retreat of the LIA. I hypothesized that brown bears in the Glacier Bay area would be genetically diverse and would exhibit genetic structure that would correspond with landscape features, in particular marine fjords and glacier covered mountains, which would inhibit gene flow. Further, because the colonization of northern Glacier Bay was recent (glaciated <150 ybp) and the landscape fragmented, I expected to be able to determine the source populations of the recent colonizers using nuclear genetic markers.

Assessing population structure of brown bears in the park provides an important part of understanding mammalian connectivity, which may help park wildlife managers reduce anthropogenic barriers to gene flow and make sound management decisions regarding bear conservation and bear-human conflict. Determining barriers and connectivity between the Park and the Preserve may have implications on managing both habituated and hunted subpopulations. Identifying potential biological corridors will help inform the park's upcoming Backcountry Management Plan by steering human use away from these areas thereby increasing the protection of brown bears as well as the safety of people. Learning the origins of Glacier Bay brown bear immigrants may shed light on colonization patterns of other recent mammalian colonizers. In addition, determination of landscape features that limit brown bear genetic connectivity in a region with very little human development may help differentiate natural from anthropogenic fragmentation in disturbed landscapes.

Methods

Study area

The study area was a 37,017 km^2 area in northern Southeast Alaska including Glacier Bay National Park and Preserve (GBNPP) and adjacent mainland United States National Forest (USFS), British Columbia Provincial Park, and private lands to the north and east (Fig. 2.2). The climate is characterized by cool summers and wet winters and topography consists of rugged mountains up to 4,633 m elevation, ice fields with glaciers extending to tidewater, and glacially carved mountains and valleys (Boggs et al. 2008). Marine waters cover 6278 km^2 (17%) and ice and snow covers 12051 km^2 (33%) of the study area (Fig. 2.3; Terrestrial Ecosystems database; Albert and Schoen 2006). The study area encompasses a wide variety of landscape features, including: the Yakutat forelands and lower portion of the large glacial-fed Alsek River on the north, Gulf of Alaska shoreline on the west, Icy Strait shoreline on the south, Chilkat Mountains and Lynn Canal on the east, and the Fairweather Mountain Range and Glacier Bay in the center.

Bear food resources vary substantially across the study area. Plant successional stages documented in Glacier Bay following glacial retreat include: pioneer communities of algae/lichen, seral forbs, and *Dryas drummondii* in areas de-glaciated within 50 ybp; open and closed scrub from 50-100 ybp; young forests from 100-300 ybp; and a mature community of old growth forests with *Sphagnum* muskegs in areas that remained ice-free during the LIA (Chapin et al. 1994). Early pioneer stage plants offer few food resources to bears, but open scrub habitats often contain a mosaic of bear foods including soapberry (*Shepherdia canadensis)*, strawberry (*Fragaria chiloensis*), locoweed (*Oxytropis campestris)*, and bear root (*Hedysarum alpinum)*. Closed scrub habitats dominated by willow (*Salix* spp.) often contain extensive soapberry, while alder-dominated (*Alnus* spp.) closed scrub contains little high-quality bear forage with the exception of groundcone (*Boschniakia rossica*), an alder root parasite (Pojar et al. 1994). Young forests in the southern portion of the Glacier Bay are dominated by dense (>60% canopy cover) Sitka spruce (*Picea sitchensis*) with little understory. Several berry-producing species

including blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and red elderberry (*Sambucus racemosa*) grow in limited abundance in young forest openings and fringe. Areas surrounding Glacier Bay that were not glaciated during the LIA consist of old-growth hemlock (*Tsuga heterophylla*) and spruce forests with interspersed peat muskegs. Old-growth communities often contain dense understories of berry-producing plants including blueberry, salmonberry and devil's club berries (*Oplopanax horridus*). Skunk cabbage (*Lysichiton americanus*) is also common in wet areas. Old-growth forests are open (<60% canopy cover) or closed, and support important spring sedge (*Carex* spp.) habitat. Riparian zones host seasonal anadromous fish runs that increase in diversity with number of years since glaciation (Milner et al. 2000). A large portion of the coastline throughout the area is bordered by recently uplifted graminoid and herbaceous beach meadows. Bear food resources in these meadows include strawberry, nagoonberry (*Rubus arctica*), dandelion (*Taraxicum* spp.), horsetail (*Equisetum* spp.), angelica (*Angelica lucida*), cow parsnip (*Heracleum lanatum*), beach lovage (*Ligusticum hutenii*), pacific hemlock-parsley (*Conioselium chinense*), and grasses. In addition to the diversity of bear plant foods available, intertidal food sources available to bears along the shoreline include acorn barnacles (*Balanus* spp.), mussels (*Mytilus trossulus*), and rock gunnels (*Stichaedae/Pholidae*). Other potential prey species throughout the study area include moose (*Alces alces*), mountain goats (*Oreamnos americanus*), voles (*Myodes* and *Mycrotus* spp.), and ground-nesting birds.

GBNPP is managed by the National Park Service (NPS). Although hunting is not permitted in the park, the National Preserve was created under Alaska National Interest Lands Conservation Act (ANILCA) and traditional subsistence and sport hunting of bears and other animals is allowed (Fig. 2.2). Similarly, hunting is allowed on the United States Forest Service, state and private lands to the northwest and east of the park and the Canadian Tatshenshini-Alsek Park land directly north. The study area encompasses the villages of Yakutat and Gustavus (<500 people each) and small (<20 people) seasonal fish camps along the Gulf of Alaska coast north of the park. The rest of the study area is essentially devoid of human development. While the shoreline of Glacier Bay receives a

limited amount of human recreational use in summer (750-1500) backcountry visitors annually) the marine waters of Glacier Bay receive over 400,000 visitors via motorized vessel, mainly cruise ships. (NPS unpublished data). Access to the park is by airplane or boat.

Sample collection

I collected bear hair from the coastal portion of 40 watersheds chosen randomly across 5 strata based on number of years since glaciation in Glacier Bay National Park from 2009-2010. Hair was collected from rub trees with or without stapled 30-40 cm pieces of barbed wire to facilitate hair collection, or opportunistically along trails or in beds. In addition, I also obtained 1) hair samples opportunistically from rub trees in remote areas of the park gathered by park personnel, researchers, and guides; 2) foot-pad tissue samples of harvested brown bears from Alaska Department of Fish and Game employees in Yakutat and Haines in the spring and fall of 2010; and 3) previously collected samples (Partridge et al. 2009). Samples were collected from six general geographic areas separated by marine water and/or mountains: east arm of Glacier Bay (East GB), Icy Strait east (Icy East), Icy Strait west (Icy West), west arm of Glacier Bay (West GB), Yakutat forelands (Yakutat), and Haines area (Haines) (Fig. 2.3).

Genotyping

All samples were sent to Wildlife Genetics International (Nelson BC, Canada). DNA was extracted with QIAGEN's DNeasy tissue kits (qiagen.com). DNA amplification and genotyping was performed in accordance with Paetkau et al. (1998). Species determination was a sequence-based analysis of a portion of the 16S rRNA mitochondrial gene (Johnson and O'Brien 1996). Samples with strong mitochondrial results were individually identified using 6 highly variable microsatellite markers and one gender marker. Microsatellite genotyping was extended for each identified individual using 21 loci. Markers examined in analysis included: G10B, G1D, G10J, G10M, MU50, MU59, G10U, REN145PO7, G10C, CXX20, G10H, MSUT2, G10P, G1A, CPH9, CXX110, MU23, G10L, G10X, and Mu26. Genotyping errors were reduced through computerized

comparison of all pairs of unique genotypes to identify and correct potential allelic dropout. Further error-reducing techniques were in accordance with methods of Paetkau (2003).

Population-structure analysis

I tested loci for deviations from Hardy-Weinberg equilibrium (HWE) using Fisher's method with 20 Markov-chain batches and 5000 iterations per batch in Genepop (Raymond and Rousset 1995). I tested for linkage disequilibrium and determined rarefacted allelic richness using Fstat (Goudet 1995). I calculated the number of alleles, effective alleles, observed and expected heterozygosity, and F_{is} by sampling location and population; probabilities of identity (PI and PI_{sibs}) (Paetkau and Strobeck 1994); and clustered samples in a principle component analysis (PCA) with GenAlEx version 6.4 (Peakall and Smouse 2006). To quantify genetic differentiation between sampling areas, I examined global and pairwise Fixation index (F_{st}) (Wright 1931, Weir and Cockerham 1984) with FSTAT and because F_{st} is limited in range in populations with high heterozygosity, I also used DEMEtics package in program R (Gerlach et al. 2010) to determine the differentiation index, D (Jost 2008).

I inferred the number of genetically distinct populations or genetic clusters (K) and individual proportional population assignments to each cluster (q) using Bayesian allele frequency assignment tests in program Structure 2.3.3 (Pritchard et al. 2000). I chose the admixture model with correlated allele frequencies between populations and ran five replicates of 200,000 Markov-chain Monte Carlo (MCMC) randomizations after 100,000 repetition burn-in for each value in a range of K = 1-12. I considered the plateau of the maximum log likelihood, L(K) (Pritchard et al. 2000), the change in likelihood, Δ K (Evanno et al. 2005), and the number of admixed individuals to determine the most biologically realistic number of populations. I also inferred population structure in a spatial explicit context with Baysian model and MCMC simulations with Geneland package (Guillot et al. 2005a) of program R (R Development Core Team 2006). Unlike program Structure, Geneland incorporates spatial coordinates of sample sites into the

MCMC simulations to determine the number of genetic groups and to define geographic boundaries for each group (Guillot 2005b). I chose a spatial model with uncorrelated allele frequencies for 1,000,000 iterations with each 1000th iteration saved for K = 1-5 based on initial Structure results. I selected a spatial coordinate uncertainty of 5000 m because brown bears are highly mobile and capable of moving this distance in a single day. I post-processed at 50 X 50 pixels with 200 burnin and determined the most likely K from the posterior distribution, and then re-ran the spatial model with correlated allele frequencies at that number of clusters to obtain individual population assignments. Based on assignment tests from programs Structure and Geneland, I assigned individuals to groups in which their ancestry (q) was highest. Individuals with maximum assignments of $q < 0.8$ were considered admixed (Bergl and Vigilant 2007, Shafer et al. 2010b). For each genetic cluster, I identified the geographic extent by calculating the kernel density (sample points/km^2) in Geographic Information System (GIS) Spatial Analyst (ESRI ArcGIS 10.x. Redlands, CA, USA) and identified potential dispersers as bears with the majority of their population assignment outside of this range.

Landscape-genetics analysis

In order to test correlations between the genetic relatedness of bears and the landscape, I developed a suite of landscape models. I used ArcGIS to generate landscape raster data at 25m grid cell size, which was ultimately increased to 200m grids due to computer processing limitations. Land cover types were determined from Terrestrial Ecosystems database (Albert and Schoen 2006) classified as conifer forest, non-forest vegetation, tidelands/marine, ice and snow, rock, non-vegetated other, freshwater, and marine. The marine waters of Glacier Bay were not included in this database, so portions of a National Oceanic and Atmospheric Administration (NOAA) bathymetry marine layer were added. Terrain rugosity was calculated for the terrestrial portion of the study area by dividing the surface area of each DEM grid cell by the planimetric area using source digital elevation models (DEM) and GIS extension DEM Surface Tools v.2.1.254 (Jenness 2010).

I generated distance and landscape models to test for isolation by resistance (IBR; McRae 2006), isolation by distance, (IBD), and isolation by barrier (IBB). I used cost-distance and least-cost path distances generated in Landscape Genetics extension for ArcGIS (Etherington 2010) for all bears and specifically for females. The two methods I applied differ in that cost–distance values are generated by simply adding the cell values between each pair of sample locations whereas least-cost paths add the cell values of the lowest cost route between sampling locations (Fig. 2.3). Both methods rely on the development and testing of landscape resistance models by generating cell value costs associated with different terrain features. Because no telemetry or GPS data exist for long-range movements of brown bears in Glacier Bay, I used results from previous studies on ursid species in the region to examine landscape features that appeared to best explain the genetic differentiations in the assignment tests of this study to inform the models. The primary landscape features believed responsible for maintaining population structure in bears in coastal Alaska include ice fields/glaciers and marine waters/fjords (Paetkau et al. 1998, Peacock et al. 2007, Proctor et al. 2012). I generated seven IBR models incorporating higher resistance values for combinations of ice, marine, and rock land cover as well as terrain rugosity (Table 1.1). All resistance models were scaled between 1 and 100 to maximize differentiation between resistance values and consistency between models. I conducted raster calculation and reclassification using ArcGIS Spatial Analyst. I generated cumulative resistance value matrices of direct-cost distances between each pair of sampling locations for all models using the Landscape Genetics extension for ArcGIS. I also fit a model of isolation by distance (IBD) using pairwise Euclidean distance and genetic relatedness in the Landscape Genetics extension for ArcGIS. I generated a single Isolation by Barrier (IBB) model that contained polylines buffered to 5 km with high resistance (1000) through the southern portion of Glacier Bay fjord and the Fairweather and the Chilkat Mountains. I used GenAlEx to calculate the Lynch and Ritland (1999) estimator. I conducted Mantel tests in the Ecodist package (Goslee and Urban 2007) of program R to examine correlations between all models of landscape distances or resistances and genetic relatedness.

Results

A total of 337 brown bear hair samples and 19 foot pad samples were analyzed. Extended genotypes were obtained for 52 brown bears from hair samples collected during this study, 35 from a previous study (Partridge et al. 2009), 17 bears from legal harvests, and 1 bear from illegal harvest for a total of 105 individuals (Fig. 2.4). The samples included 66 males and 39 females for a male-biased sex ratio of 1.69 males per female.

Population structure

I found no significant deviations from Hardy-Weinberg equilibrium or evidence of genotypic linkage disequilibrium ($p < 0.05$) by loci indicating that loci are neutral and independent of one another. Samples from West GB (n = 49), which had the highest mean number of alleles, effective alleles, and allelic richness rarefacted to account for sample size (Table 2.2). Bears sampled in Icy East had the greatest observed heterozygosity (n=10) while bears from Haines had the highest mean expected heterozygosity and the lowest sample size (n=5). The PI was $<1.0 \times 10^{-17}$ whereas PI_{sibs} was 1.1×10^{-07} at 21 loci. Principal components analysis indicated a distinct genetic discontinuity between Icy West-Yakutat bears and bears from all other sampling locations on coordinate axis 1 (Figure 2.5). Similarly, coordinate axis 2 indicated another distinct discontinuity between Icy East-Haines bears and the surrounding groups. The majority of bears sampled in East GB appeared to group with the Icy East-Haines group with several exceptions, whereas West GB bears overlapped with both other groups but also occupied a distinct zone (lower right quadrant) of coordinate space.

Structure results indicated two or three distinct genetic groups (K) within the study area. At K=2 there is a strong split between the west (Icy West and Yakutat) and east (Icy East and Haines) sides of Glacier Bay, with East GB and West GB bears deriving the majority of their ancestry from the eastern group (Fig. 2.6a). At K = 3, a third population emerges largely dominated by bears sampled in West GB (Fig. 2.6b). At K = 4, a less discrete population emerges and many individuals were assigned mixed ancestry, indicating that the program may have exceeded the true number of genetic

subdivisions (Fig. 2.6c). At K = 5 most individuals showed admixed ancestry indicating biological reality has been exceeded (Fig 2.6d). Using the Pritchard et al. (2000) method of allowing the highest log likelihood of the data (L(K)) with the lowest variance to determine the number of genetic groups indicated 5 populations (Fig. 7a). Using the Evanno et al. (2005) method of allowing the drop in Δ K to determine the number of genetic groups indicated 2 populations (Fig. 2.7b). Posterior distributions calculated in Geneland varied between 2 and 3 distinct populations. Despite L(K) results, at K = 4 the number of biologically meaningful number of clusters appears to have been exceeded . In Structure K = 3, only 13 (12%) out of 105 individuals showed admixed assignments whereas at K = 4, 36 (34%) individuals showed admixed assignments. This proportion of admixed individuals is not realistic with so few purebred parents. Hence I considered K = 2 and K = 3 competing models for describing genetic diversity of brown bears in this study area. The K = 2 model divided bears into East and West groups, while the K=3 model divided bears into East, West, and GLBA (Glacier Bay) groups (Table 2.3). Structure K=2 results assigned the majority of bears sampled in Icy West and Yakutat into the West group, and all other sampling regions into the East group (Table 3a). Structure K=3 results differed in assigning a large portion of bears from East GB (q=0.31) and the majority of bears from West GB (q=0.53) to the GLBA group (Table 2.3b). Geneland K=3 results assigned the majority of bears sampled in East GB (q=1.00) and West GB (q=0.82) to the GLBA population (Table 2.3c). Kernel density maps showed that the geographic range of the two groups identified by Structure K=2 overlap in much of Glacier Bay (Fig. 2.8). Density maps of the range of groups indicated in Structure K=3 showed that the GLBA group lies geographically within the East group and that all three groups overlap in the northwest portion of Glacier Bay (Fig 2.9 and 2.10). While K=2 is a competing model, there is strong evidence of substructure within the K=2 East group, including the unique coordinate space occupied by most bears sampled in West GB in the PCA analysis (Fig. 2.5). The third population (GLBA) did not appear to be an admixture between the East and the West groups because all 29 individuals assigned to GLBA genetic group in Structure at K=3 were assigned to the

East group at K=2 and only one out of 29 was admixed (Table 2.3 a and b). Population assignments differed substantially in the Geneland spatial model in which bears sampled in East GB were assigned exclusively to the GLBA population instead of the majority assigned to the East population (Table 2.3b and c). While the numbers of individuals assigned in the West population was similar between Structure and Geneland, Structure assigned 16 more bears to the East population than Geneland while Geneland assigned 19 more bears to the GLBA population than Structure. The greatest proportion (0.17) of admixed ancestry occurred in the GLBA population.

I found significant genetic differentiation between sampling areas based on F_{st} and Jost's D estimates (Table 2.4a). F_{st} estimates ranged from 0.016 to 0.083 and D values ranged from 0.029 to 0.211. F_{st} estimates indicated 9 significant pairwise comparisons while D estimates indicated 10 significant out of 15 total comparisons. For both metrics, the largest significant differences were found between Icy East and Yakutat, and Icy East and Icy West. Pairwise F_{st} and Jost's D values also indicate significant differentiation between all of the identified populations at K=3 (Figure 2.10 and Table 2.4b) despite geographic overlap. At K = 3, the East group had the greatest number of effective alleles, allelic richness, expected heterozygosity and number of private alleles while the GLBA group had the least (Table 2.5). During this study, I recaptured 27 bears, of which 21 were male and 6 were female. Two recaptures occurred across two sampling areas and I assigned these individuals to the sampling area with the lowest sample size. The longest movement between capture locations was undertaken by a female who traveled 76 km (direct line) from East GB to Icy West between July 2009 and June 2010, and then 68 km by Sept. 2010 ending up 7.5 km from her original capture location (Fig.2.11). The second longest movement was by a male who traveled 57 km from northern to southern GB West from August 2009 to June 2010. Both individuals were assigned to the East population in Structure at both K=2 and K=3.

Landscape genetics

Due to computer limitations I was not able to generate least-cost paths for all 105 brown bears, so I generated cost-paths for all bears and least-cost paths for females only (n = 39). All seven IBR, both IBD, and the single IBB models were significantly ($p<0.001$) correlated with patterns of genetic diversity in both cost-distance and least-cost paths (Fig. 2.12). In cost-distance analysis of all bears, Ice, Rug, and Rug_ice_mar models (Table 2.1) explained the greatest amount of variance ($r=0.48$-0.49) in genetic diversity. In least-cost path analysis of females only, the Ice_mar and Rug_ice_mar models explained the most variance with correlation coefficients of 0.48 – 0.50. No single model performed significantly better than the rest, but Mantel *r*-values for cost-distance Mar and Ice_mar models were lower than top models at 95% confidence intervals. Hence these results do not show that IBR or IBB models explain genetic diversity better than IBD models.

Discussion

Population structure

There is a distinct genetic split between brown bears sampled on the east versus the west side of southern Glacier Bay. This pattern is especially apparent from the geographic distribution of assignments from program Structure K = 2 (Fig. 2.8). Yakutat to Icy West is almost exclusively populated by the West group while Haines to Icy East is entirely comprised of the East group and northern Glacier Bay is dominated by the East group with significant presence of the West group. Fst and Jost's D values are highest between groups on opposite sides of Glacier Bay (Table 2.4). At K=3 additional substructure within the East population is apparent and the majority of bears in the West GB and a large proportion from the East GB carry a unique genetic signal (GLBA) that is distinct from the Yakutat/Icy West and the Haines/Icy East groups (Figs. 2.9 and 2.10, Table 2.3). L(K) has been shown to split populations into too many clusters while Evanno's Δ K is more accurate in identifying numbers of subpopulations, except in a situation of multiple subpopulations on either side of a contact zone (Evanno et al. 2005). Contact zones are

often characterized by geographic overlap of populations leading to genetic admixture. Northern Glacier Bay appears to be an area of genetic confluence whether the number of distinct genetic groups is two or three. At K=2 the majority of bears sampled in Northern Glacier Bay are assigned to the East group but the West population contributes substantial ancestry. At K=3 the third (GLBA) population further divides the proportions of assignments of bears from northern Glacier Bay (Table 2.3). It is plausible that this portion of Glacier Bay represents a contact zone with geographic overlap and admixture between the GLBA, East, and West groups, hence the Evanno method of determining K failed to detect the substructure between the East and GLBA groups. As further evidence, the GLBA population, almost exclusively sampled in northern Glacier Bay, has the highest proportion (0.17) of admixed ancestries (Table 2.3a and b). Twenty-six out of 29 bears assigned GLBA ancestry were sampled in West GB, and only one bear (male) assigned to the GLBA population was sampled in Icy West, and none in Yakutat, indicating little genetic movement from the GLBA population to the West. All of the bears (100%) sampled in the Yakutat sampling area, including those in the National Preserve, were assigned to the West population, so genetic movement of bears between the Preserve and Glacier Bay is not supported. Similarly, all bears sampled in Haines were assigned to the East population, indicating that GLBA bears do not disperse in an easterly direction either. Conversely, 38% of the ancestry in West GB and 51% of the ancestry in East GB was derived from the East group, indicating the majority of gene flow comes from the east into Glacier Bay. In light of such genetic confluence and admixture, the detection and maintenance of the third GLBA population is curious.

Population sources

I propose that the East and West genetic groups detected in this study represent contemporary colonizing sources of Glacier Bay, and the third GLBA group represents a historic colonizing or ghost population. The East and West groups extend to Yakutat and Haines respectively, with 100% assignments in those areas. Neither the Yakutat forelands nor Lynn Canal was completely glaciated during the LIA indicating likely areas

of source populations for the recolonization of Glacier Bay. The most likely explanation is that the GLBA group originated from a small colonizing population that experienced enough genetic drift over time to develop its unique genetic signal. Lower allelic richness, heterozygosity, and number of private alleles in this population indicates afounder effect or population bottleneck (Table 2.5). Low effective population size hastens genetic drift and subsequent changes in genetic structure (Wright 1943). The effective population size of early bears recolonizing the Glacier Bay shoreline was likely quite low due to glacial movement barriers and low female dispersal so a founder effect in this colonizing population seems plausible. A second pulse or recent immigration would contribute to the presence of individuals from other genetic groups in northern Glacier Bay. The original colonizing population may have been from the East (as evidenced by lower F_{st} between GLBA and East (Table 2.4b) or from a small refugial or ghost population. It is possible that the GLBA population is part of an un-sampled contemporary population on the Alsek River corridor to the north. Only one sample from this area was obtained from the upper Alsek River in this study and that individual derived 91% of her ancestry from the East group. The Alsek River corridor, however, reaches the ocean in the National Preserve, where nine samples were collected, all with strong West assignments. The distance between the single "East" bear on the upper Alsek and the nine "West" bears at the mouth is approximately 63 km, separated by a large glacial lake (Alsek Lake) that may impede movements. Further sampling in this region may reveal more insights into the origins of the GLBA group. Despite the extent of genetic overlap occurring in northern Glacier Bay, it appears that brown bear dispersal and reproduction have not been sufficient since colonization to eliminate the structure from this original colonizing population. If the influx of bears from the East and West groups is recent and dispersers are subadults, it is possible that there has not been sufficient time for admixture to occur. Ecological niche partitioning might be explored as another possible cause of the low degree of admixture. Niche segregation has been found to promote genetic differentiation in sea lions (Wolf et al. 2008) although this has not been documented in contemporary ursids. Seasonal migrations corresponding with

mating season could be another factor in maintaining genetic differentiation, but again there is no evidence in ursids. If each population dens and subsequently mates in different geographic regions, then summer (which is when samples were collected) ranges would not affect genetic relatedness. This possibility may hold true for females with strong philopatry, but not for male brown bears that disperse from their natal range (McLoughlin et al. 1999). Regardless of the reason for low admixture, the combination of high geographic overlap of different genetic groups, substantial genetic connectivity with the East, and long-range movements observed during this study (Fig. 2.11) indicate that the unique genetic signature of northern Glacier Bay (GLBA) may soon be erased due to introgression.

Landscape influences

The strong genetic differences between bears on the east versus west sides of southern Glacier Bay indicate that the wide mouth of the fjord inhibits gene flow. Additionally, the glacier-covered Fairweather Mountains appear to inhibit gene flow between the Gulf of Alaska coast dominated by the West group and northern Glacier Bay dominated by the GLBA and East groups. Connectivity between northern Glacier Bay and Lynn Canal appears strong as evidenced by the number of individuals assigned East ancestry in both areas, indicating that the Chilkat Mountains are not as formidable a barrier as the Fairweather Mountains. Correlations with landscape models differed between all bears and females only, indicating different landscape factors influencing each sex, although differences were not significant. Lack of significantly different Mantel correlation coefficients (r) indicate that the IBR and IBB landscape models, based on landscape features shown to inhibit genetic connectivity of bears in previous studies, did not explain genetic diversity better than IBD models. It is possible that the resistance values of landscape features were modeled too broadly and were unable to distinguish fine-scale geographic variation that may influence gene flow. It is also possible that the correlations were confounded by multiple individuals with differing genotypes in close vicinity. For example, at one location in northern Glacier Bay, 11 bears were assigned to GLBA (n = 7), East (n = 3) and West (n = 1) indicating large genetic at small geographic

distances. There is a possibility of Type 1 errors associated with Mantel tests that may have artificially inflated correlations between landscape models and genetic relatedness due to multicollinearity between separation distances as well as insensitivity to non-linear relationships (Balkenhol et al. 2009). In a rapidly changing landscape, it is also possible that the current nuclear genetic diversity of brown bears in Glacier Bay is influenced more by past landscapes and their associated resistances than current landscapes. For example, 100 years ago the low elevations surrounding the west arm of Glacier Bay had been deglaciated only 50 years while the east arm of the bay was still entirely surrounded by ice (Fig. 1.1). At this time a large glacial lake in the southern east arm likely inhibited migration through the low elevation Endicott Gap (McKenzie and Goldthwait 1971, Goodwin 1988). Landguth et al. (2010) found that the amount of time it takes to detect changes in population structure is inversely related to minimum dispersal distances. While brown bears are known to disperse great distances, extensive glacier-covered mountains and marine fjords of 100 years ago would have severely inhibited movements, hence population structure from that time may still be detected today. Alternatively, genetic mixing between diverse populations of bears in Glacier Bay may be so recent that the correlations to landscape are not detectable.

The shoreline appears to be the primary migration corridor for brown bears in the study area as evidenced by a continuous population of bears from the southwest side of Glacier Bay to Yakutat and another from the southeast side of Glacier Bay to Haines. The majority of bears sampled surrounding the Endicott Gap were assigned to the East population, indicating a likely migration corridor. The proposed Tarr Inlet-Melbern Glacier corridor is not supported by these data given 100% assignment of bears at the mouth of the Alsek River to the West group, assignment of the single bear sampled from upper Alsek River to the East group, and the assignment of the majority of bears sampled in West GB to the GLBA group. More samples from the Alsek River are necessary to determine the level of movement between this valley and Glacier Bay.

The mouth of Glacier Bay, which is 6.7 km across at the mouth and approximately 18.5 km at its widest point, appears to similarly block genetic transfer and funneled dispersers northward. I propose that the recent glacial history and unique geography of Glacier Bay has created a suture zone in the northern portion of the bay. Suture zones were defined by Remington (1968) as areas of geographic overlap between assemblages of species or subspecies where admixture occurs across multiple taxa. One explanation for the formation of these zones is the postglacial range expansion of species from glacial refugia to midpoints between refugia (Anderson 1949, Remington 1968, Swenson and Howard 2005). In addition, low mountain passes tend to promote hybrid zones by providing dispersal corridors through the mountains which represent strong barriers (Hewitt 1996, 2000, Swenson and Howard 2004). Northern Glacier Bay represents a likely suture zone that formed after the retreat of ice from the LIA. This process is apparent at the population level for brown bears. Glacier Bay is surrounded by extreme topography of the ice-covered Fairweather and Chilkat mountain ranges on the east, west, and north sides, significantly limiting the potential for plant and animal migration. While the majority of Glacier Bay fjord was filled with ice only 260 years ago, portions of land masses to the east and west were not glaciated and hence served as glacial refugia (Connor et al. 2009). As the ice retreated from the south, plants and animals likely recolonized newly available terrain from both east and west refugia while Glacier Bay fjord inhibited movement of terrestrial species across the bay and funneled dispersal in a northward direction. At the northern end of Glacier Bay these populations came into secondary contact after several hundreds of years of separation. In the case of brown bears the contact zone involves three overlapping genetic groups. While the genetic signature of the brown bears in Glacier Bay provides evidence of a contact zone at a population level, genetic analysis across other taxa would determine if Glacier Bay represents a suture zone for many terrestrial species.

Effects of habitat quality

In addition to landscape influences, differing food resources across the study area may influence migration and gene flow. Paetkau et al. (1998) disproved the hypothesis that

the larger coastal brown bears were genetically isolated from smaller interior bears. Ecological factors, such as abundance of rich salmon resources on the coast vs. largely vegetative inland diets (Hilderbrand et al. 1999, Mowat and Heard 2006) explain these phenotypic differences. Glacier Bay proper is a unique coastal environment because potential salmon streams are in the process of being developed. Milner et al. (2000) found colonization, abundance, and diversity of fish species in the streams of Glacier Bay to be positively correlated to stream age, hence the majority of steep glacial runoff streams in northern Glacier Bay do not support salmon. Mowat and Heard (2006) used stable isotope analysis to assess the proportion of assimilated carbon and nitrogen coming from plant, marine, and terrestrial meat sources from a sample of seven brown bears sampled in northern Glacier Bay. Their results indicated a diet of 69% plants, 31% marine sources, and 0% terrestrial meat. The proportion of marine-derived food sources found in the diets of Glacier Bay brown bears is low compared to diets of brown bears along the coastline of British Columbia and Alaska (Mowat and Heard 2006) indicating that brown bears in Glacier Bay do not have access to as much salmon as other coastal populations. While there are no data on body mass or population metrics, using the relationships developed by Hilderbrand et al. (1999) we would expect brown bears in Glacier Bay to have body mass and productivity similar to other populations with moderate salmon consumption. By contrast, the coastal brown bears on the Gulf of Alaska have access to abundant well developed salmon streams. Preliminary comparisons of skull sizes of 1239 harvested male and female brown bears between the Yakutat forelands northwest of Glacier Bay (ADF&G game management unit 5A) and mainland bears east, north and south of Glacier Bay (ADF&G units 1C and 1D, Glacier Bay National Park excluded) show that both male and female bears on the northwest coast have significantly larger skull sizes (ADF&G 2001, Lewis 2008). Mowat and Heard (2006) found that skull size of brown bears increased with the amount of salmon in the diet. The Yakatat forelands contain well developed drainage systems that likely contain more diverse and temporally varied salmon species, as well as large seasonal runs of eulachon (*Thaleichthys sp.*). In addition, bears on the outer coast of the southeast

Alaska mainland likely benefit from increased access to fish and marine-mammal carcasses washing up on the beach from the open ocean (personal observation). Brown bear populations in North America with abundant food resources generally have smaller home-range size (McLoughlin et al. 1999). Additionally, bears, particularly males, in areas of abundant protein resources are able to grow large bodies that may preclude them from largely vegetarian diets due to higher nutritional needs (Rode et al. 2001, Robbins et al. 2004). Smaller home ranges and larger body size of the bears on the Yakutat forelands northwest of Glacier Bay may further explain why immigration/gene flow from that direction into Glacier Bay appears low. Established salmon resources also exist on the east side of the study area, but not to the same extent as the west side as demonstrated by smaller skull sizes (ADF&G 2001, Lewis 2008).

Management implications

The shoreline of Glacier Bay hosts brown bears from three distinct genetic groups. The ranges of two of these populations extend well into non-park lands to the northwest and northeast, while the range of the third population is specific to the park. Migration into the park from surrounding areas is likely, particularly from the east, while migration out of the park is not supported. However, further sampling in the Haines and Lynn Canal areas would be required to further explore migration. Genetic movement from Glacier Bay, where bears may become habituated to bear viewers, and the preserve, where hunting is allowed, is not supported. The results of this study support previously published conclusions that wide marine fjords and glaciated mountains inhibit gene flow in bears (Peatkau et al. 1998, Peacock et al. 2007, Proctor et al. 2012). Shoreline and non-glaciated valleys in a region heavily fragmented by fjords and glaciers should be considered likely travel corridors and protected from heavy human use and anthropogenic disturbance. While the landscape resistance models tested in this study were not able to distinguish the subtler landscape features that may influence genetic connectivity, these models do provide basis for further site-specific analysis.

Based on population sources of brown bears in this study, the pattern of recolonization in Glacier Bay can be inferred, and this pattern likely mirrors the recolonization of other similarly vagile mammals. As the glacier of the LIA retreated northward, dispersers colonized the southern shoreline from both east and west populations that had been separated for over 500 years. The southern Glacier Bay fjord inhibited movement across the bay and funneled dispersal to the north. In northern Glacier Bay these populations came into secondary contact with each other, and possibly other earlier colonizers of ghost populations, creating a suture zone that warrants further exploration across taxa.

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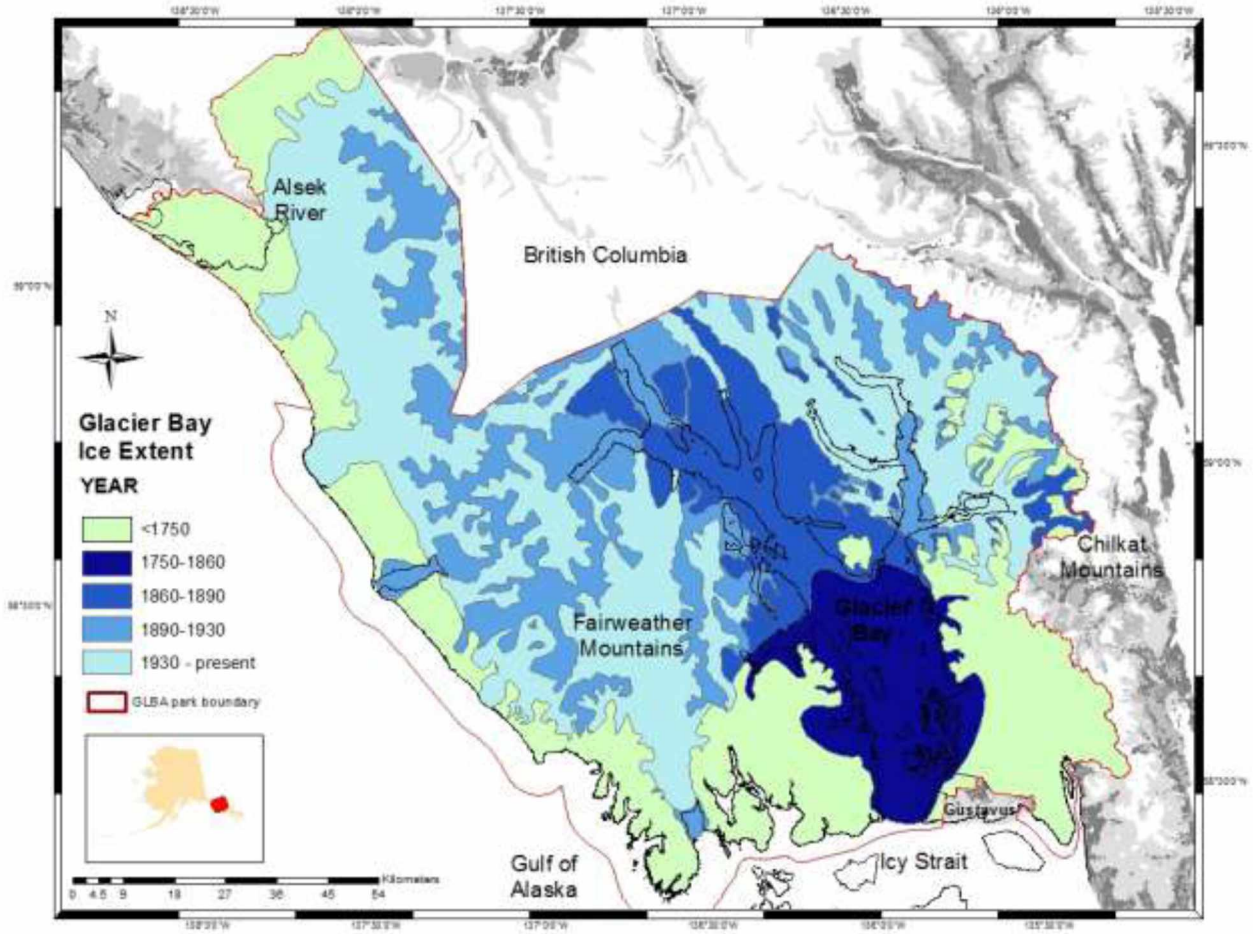


Fig. 2.1. Ice extent and retreat by year in Glacier Bay National Park and Preserve (GBNPP), Alaska, since the Little Ice Age (Geiselman et al. 1997). Land colored green has not been glaciated since the last glacial maximum (~10-12,000 ybp).

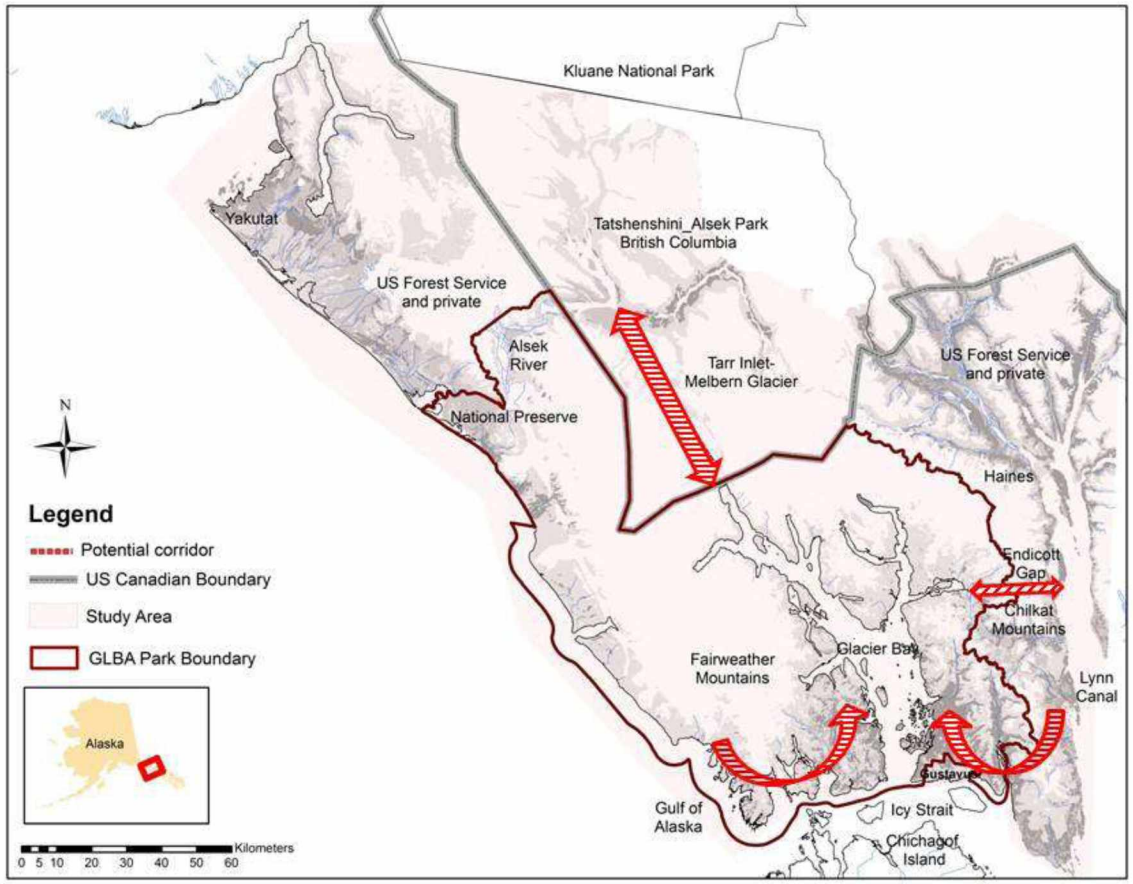


Fig. 2.2. Location of study area and possible wildlife migration corridors for brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010.

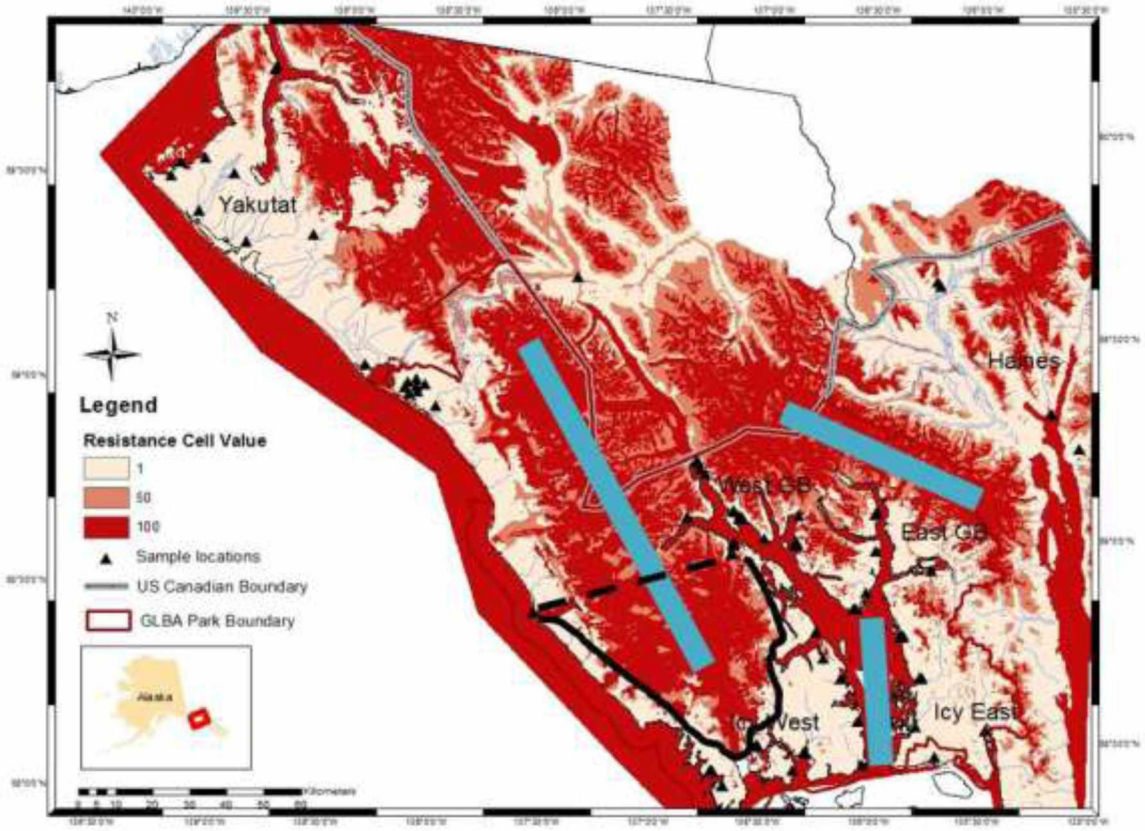


Fig. 2.3. Example of landscape resistance model (Ice_mar_rk) for testing IBR in brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010. Cell resistance values range from 100 for marine and ice, 50 for rock, and 1 for all other landcover classes. Blue rectangles indicate barriers with inflated cell values of 1000 in IBB models. Dashed black line indicates the cost-distance while the solid black line indicates the least-cost path between bear sampling locations. Raster cell size was 200m.

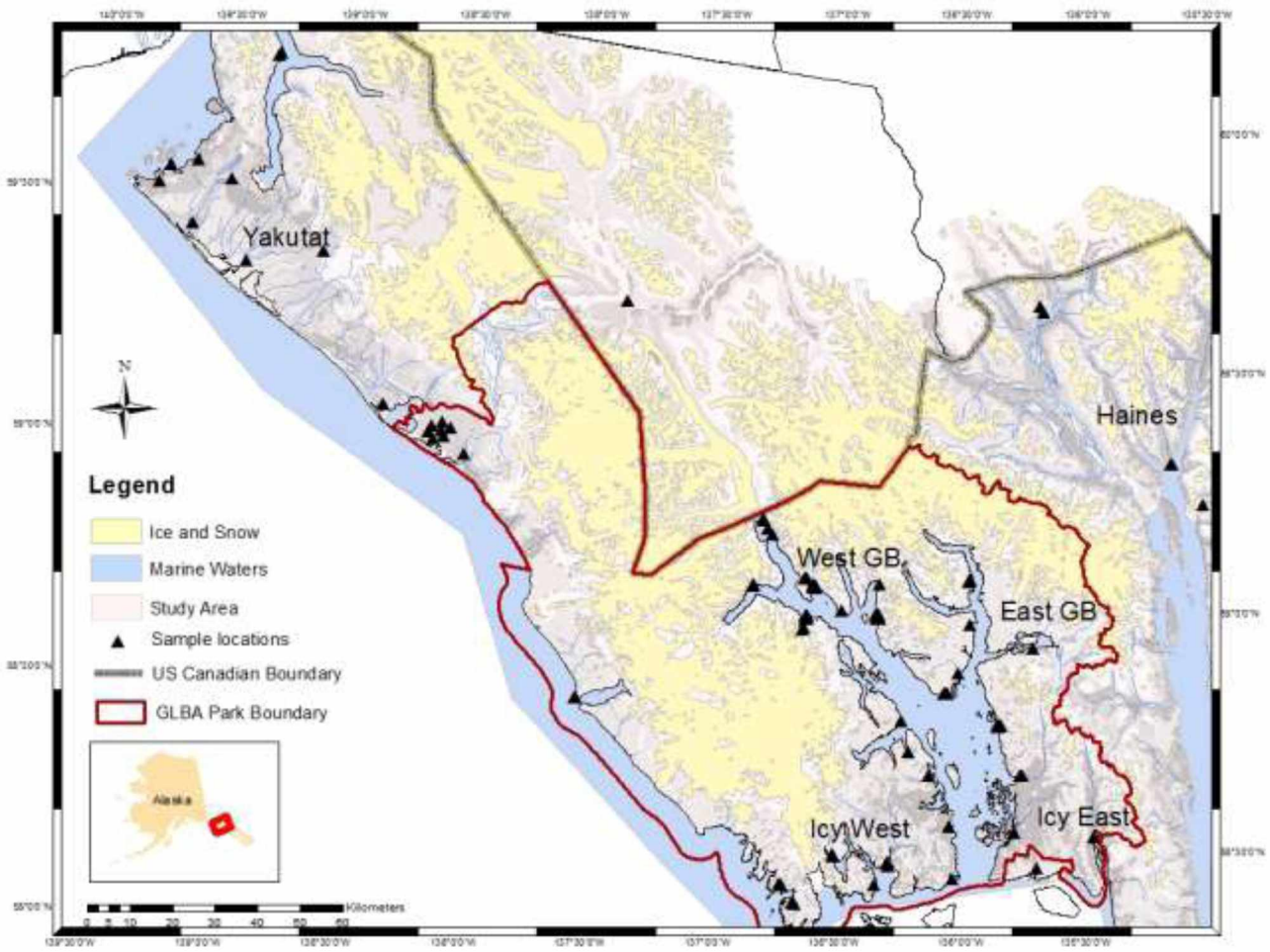


Fig. 2.4. Location of 105 brown bear genetic samples and sampling areas used in brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010.

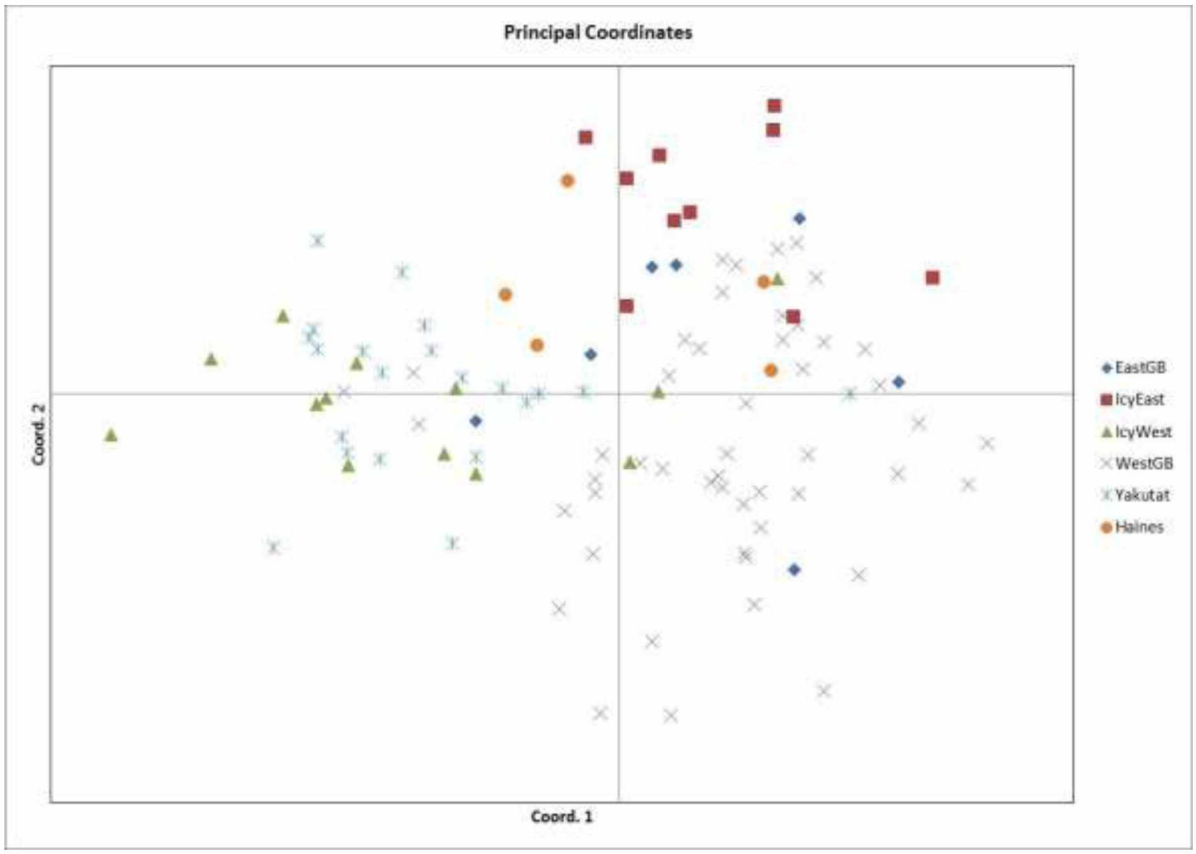


Fig. 2.5. Principal coordinate analysis of 105 individual brown bears based on 21 microsatellite loci for landscape genetics study in Glacier Bay Alaska, 2009-2010.

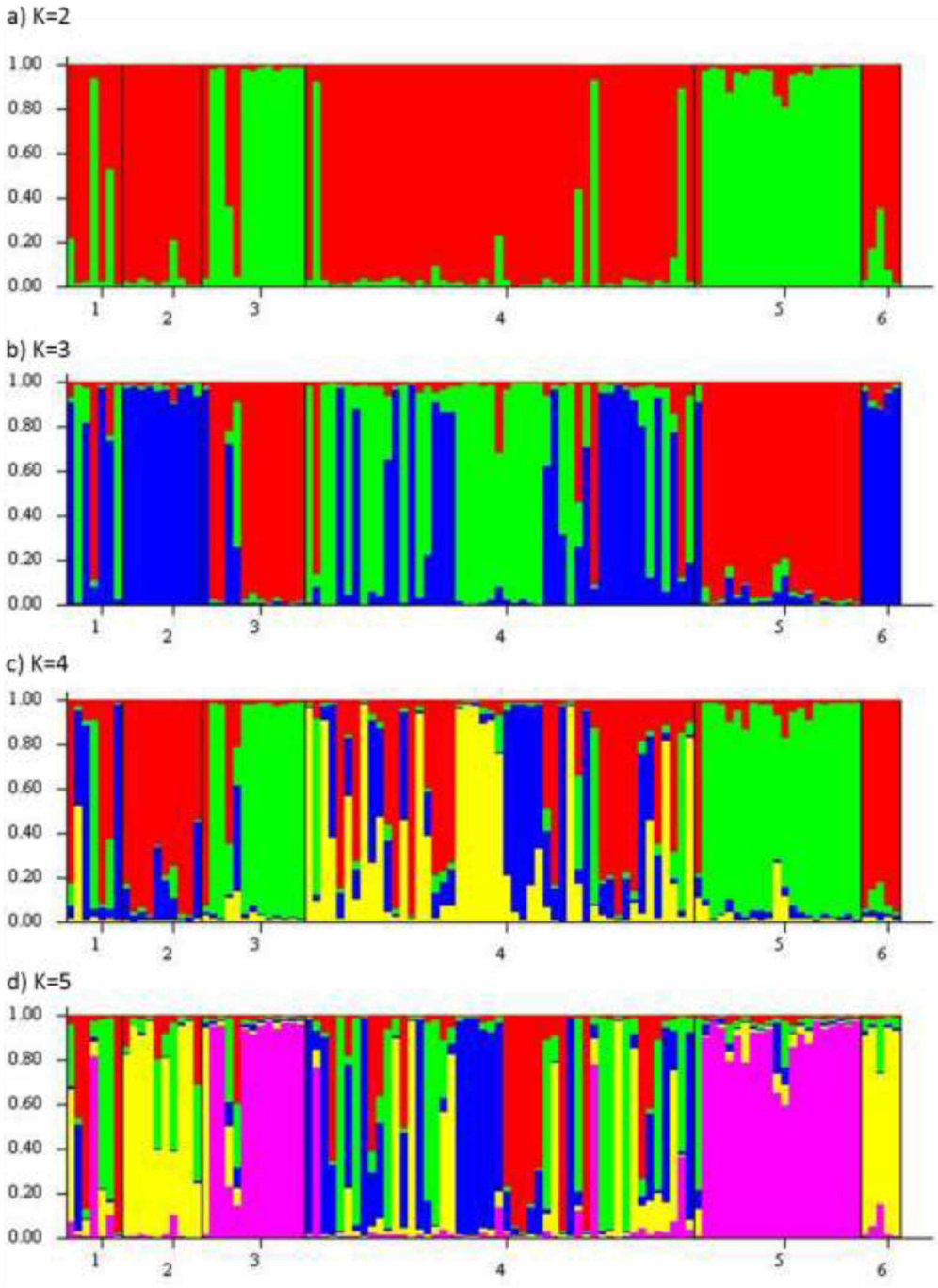
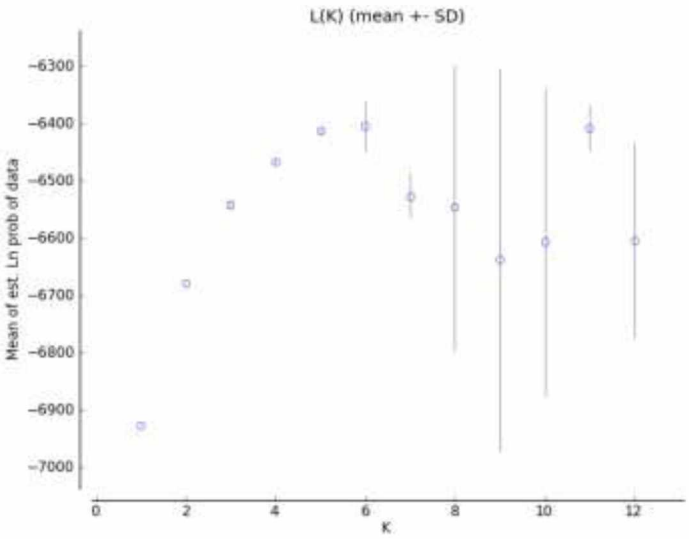


Fig. 2.6. Structure output for 105 21-loci genotypes of brown bears at K = 2 (a), K = 3 (b), K = 4 (c), and K=5 (d) with colors representing estimated ancestry in each identified population. Sample locations are as follows: 1-East GB, 2- Icy East, 3-Icy West, 4-West GB, 5-Yakutat, and 6-Haines in landscape genetics study in Glacier Bay Alaska, 2009-2010.

a)



b)

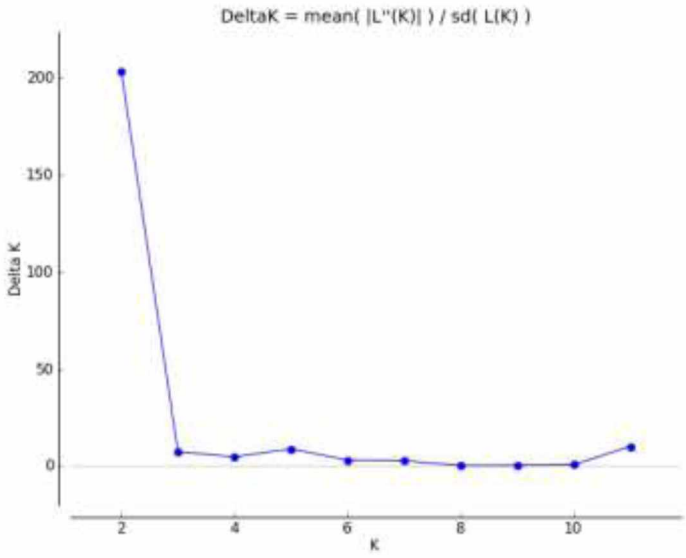


Fig. 2.7. L(K) and Δ K of genetic data from 105 individual brown bears for landscape genetics study in Glacier Bay Alaska, 2009-2010. The Pritchard et al. (2000) method of allowing the highest L(K) with the lowest variance to determine the number of genetic groups indicates five populations (a) and the Evanno et al. (2005) method of allowing the drop in Δ K to determine the number of genetic groups indicates two populations.

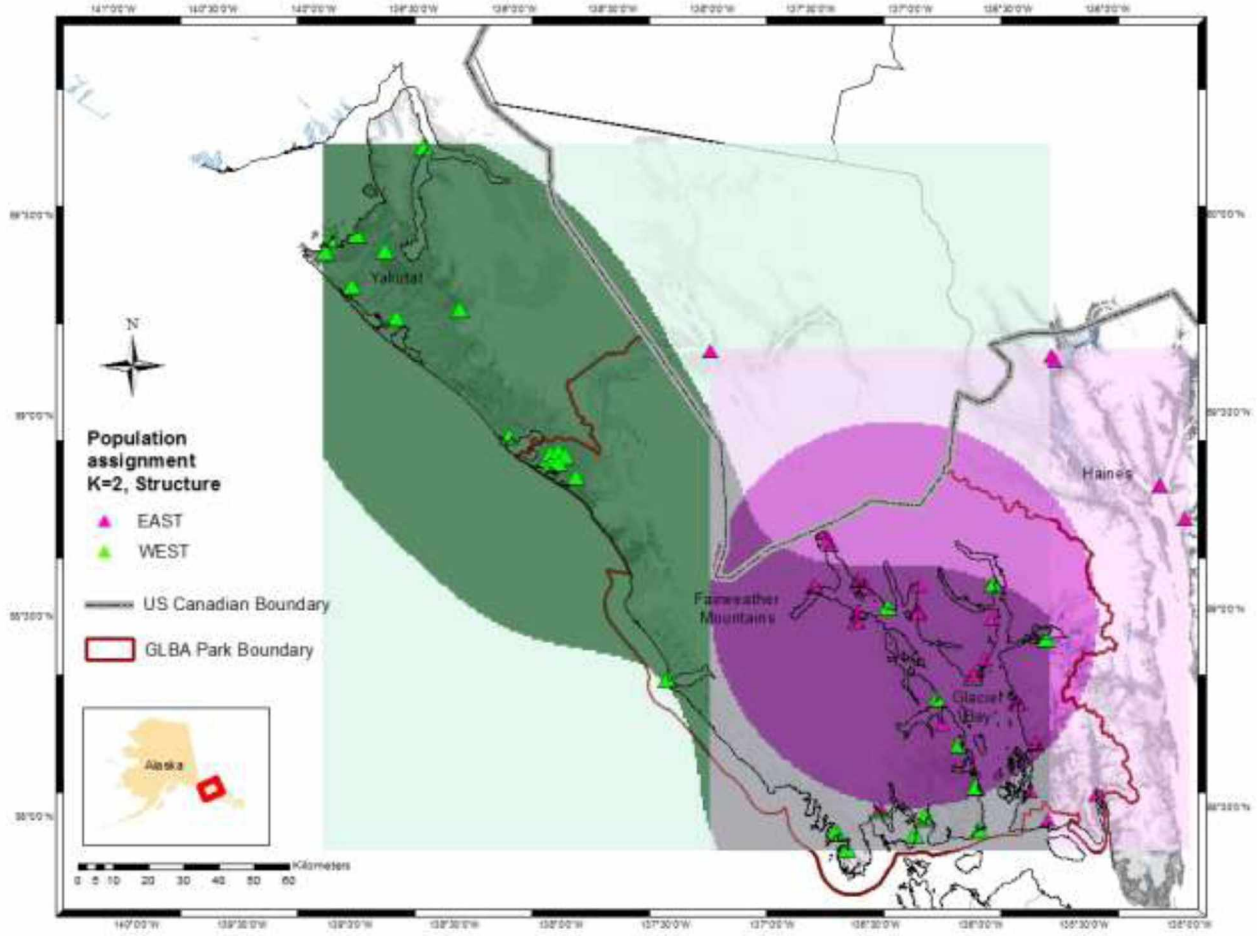


Fig. 2.8. Population assignments of 105 brown bears at K = 2 across sampling locations derived from program Structure in brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010. Shaded areas represent kernel density estimates of 0.0015-0.004 sample points per km^2 by West (Green) and East (purple) populations.

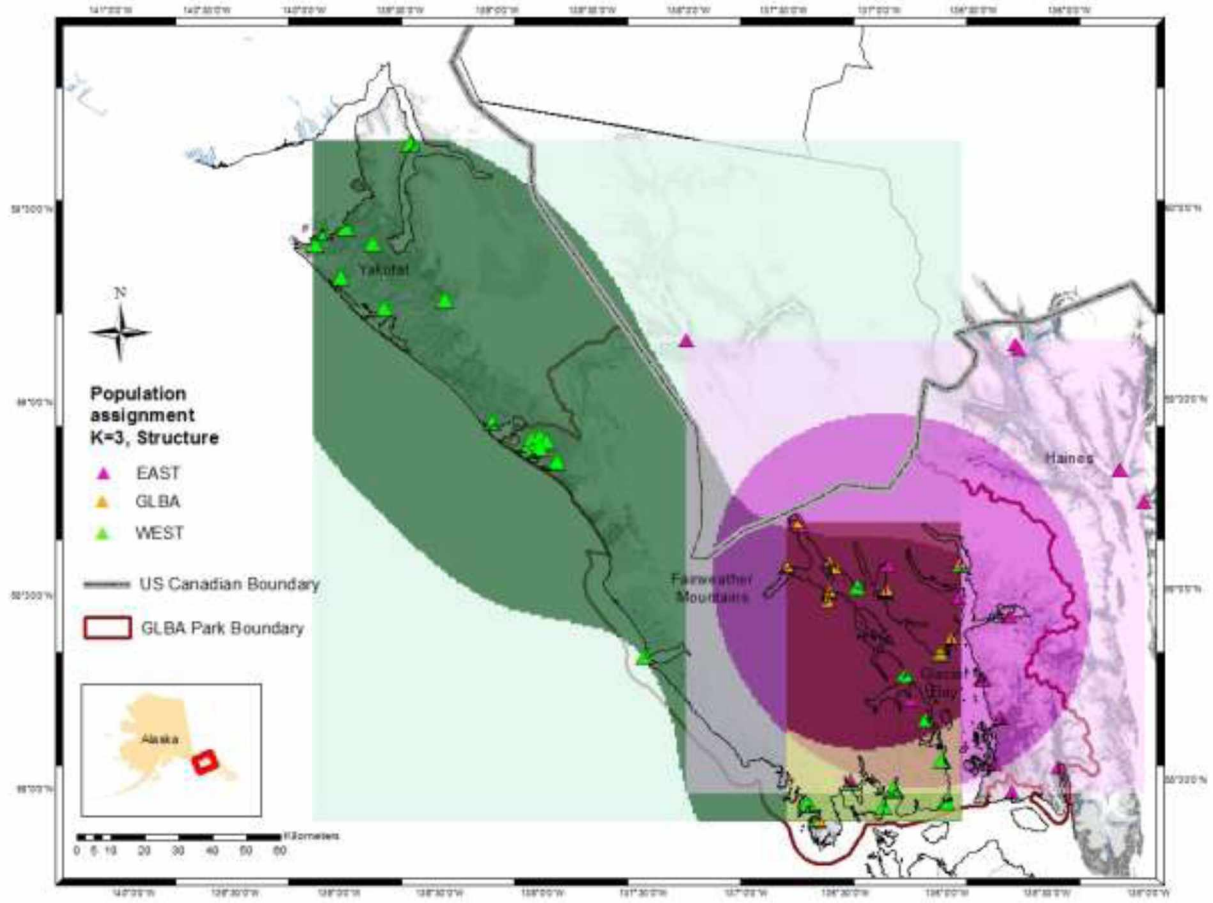


Fig. 2.9. Population assignments of 105 brown bears K=3 across sampling locations derived from program Structure in brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010. Shaded areas represent kernel density estimates of 0.0015-0.004 sample points per km^2 by West (Green), East (purple), and GLBA (orange) populations.

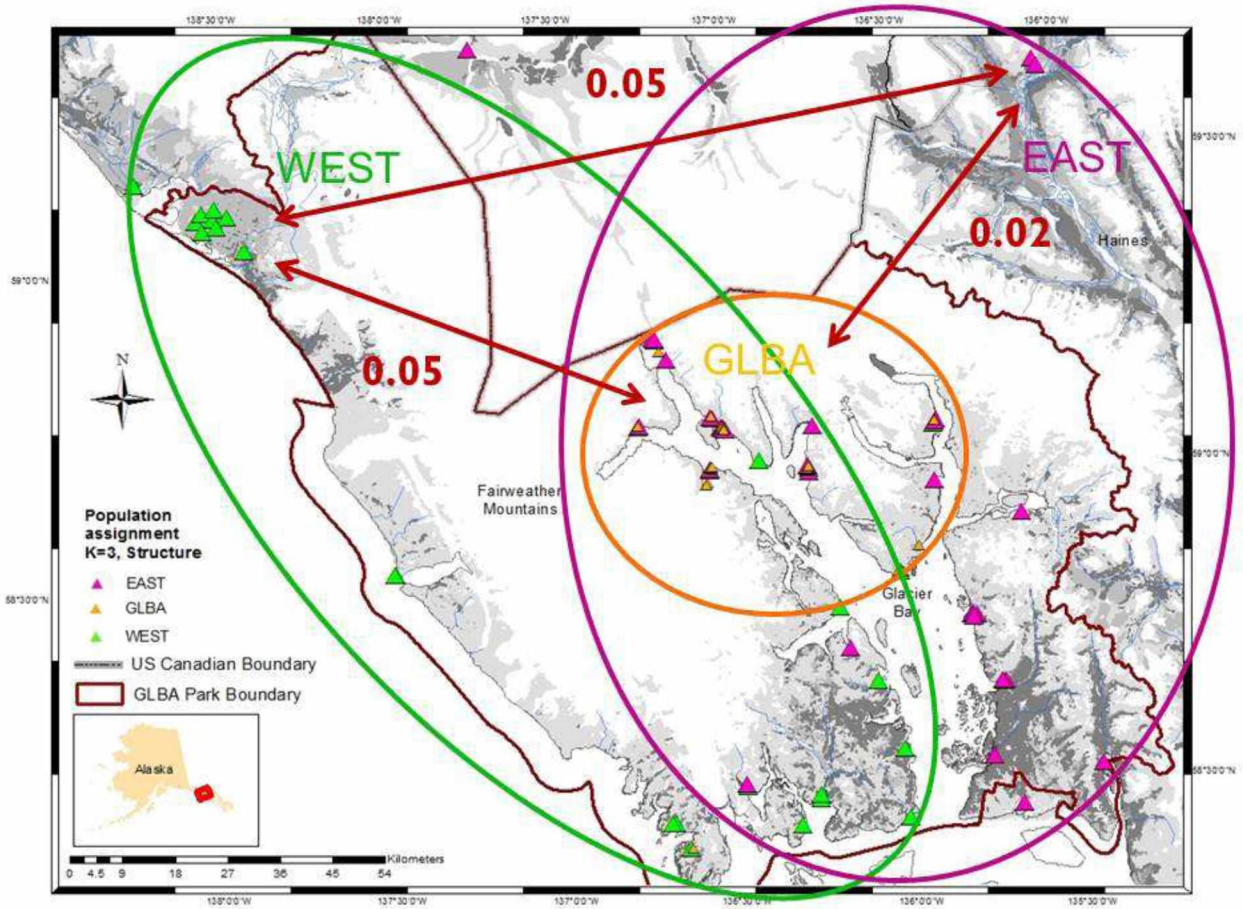


Fig. 2.10. Population assignments of 105 brown bears at K = 3 with F_{st} values across sampling locations in brown bear landscape genetics study in Glacier Bay, Alaska, 2009-2010. Red numbers indicate significant F_{st} values between populations.

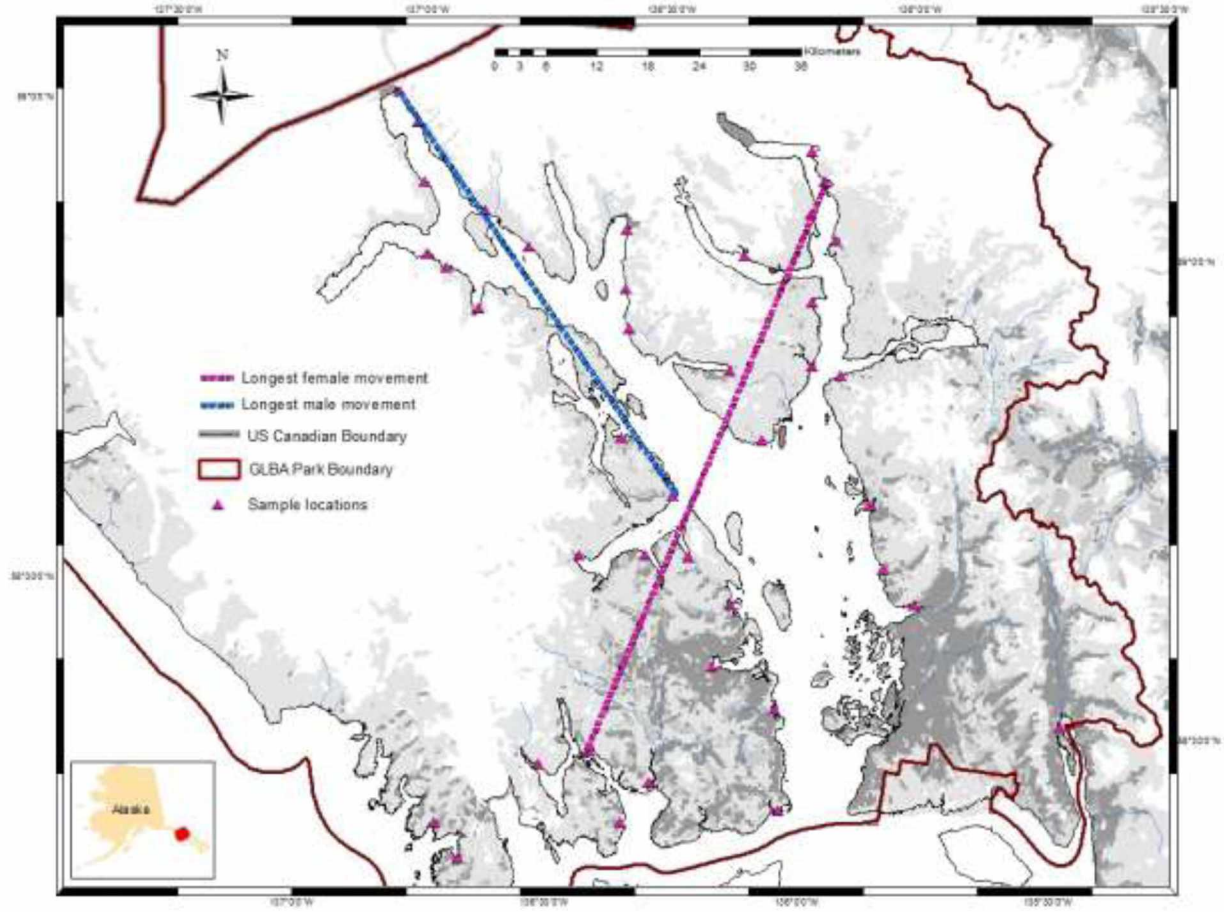


Fig. 2.11. The longest individual movements between capture locations for a female who traveled 76 km (direct line) between July 2009 and June 2010, and then 68 km by Sept. 2010 ending up 7.5 km from her original capture location (Fig.8) and a male who traveled 57 km from August 2009 to June 2010, Glacier Bay, Alaska.

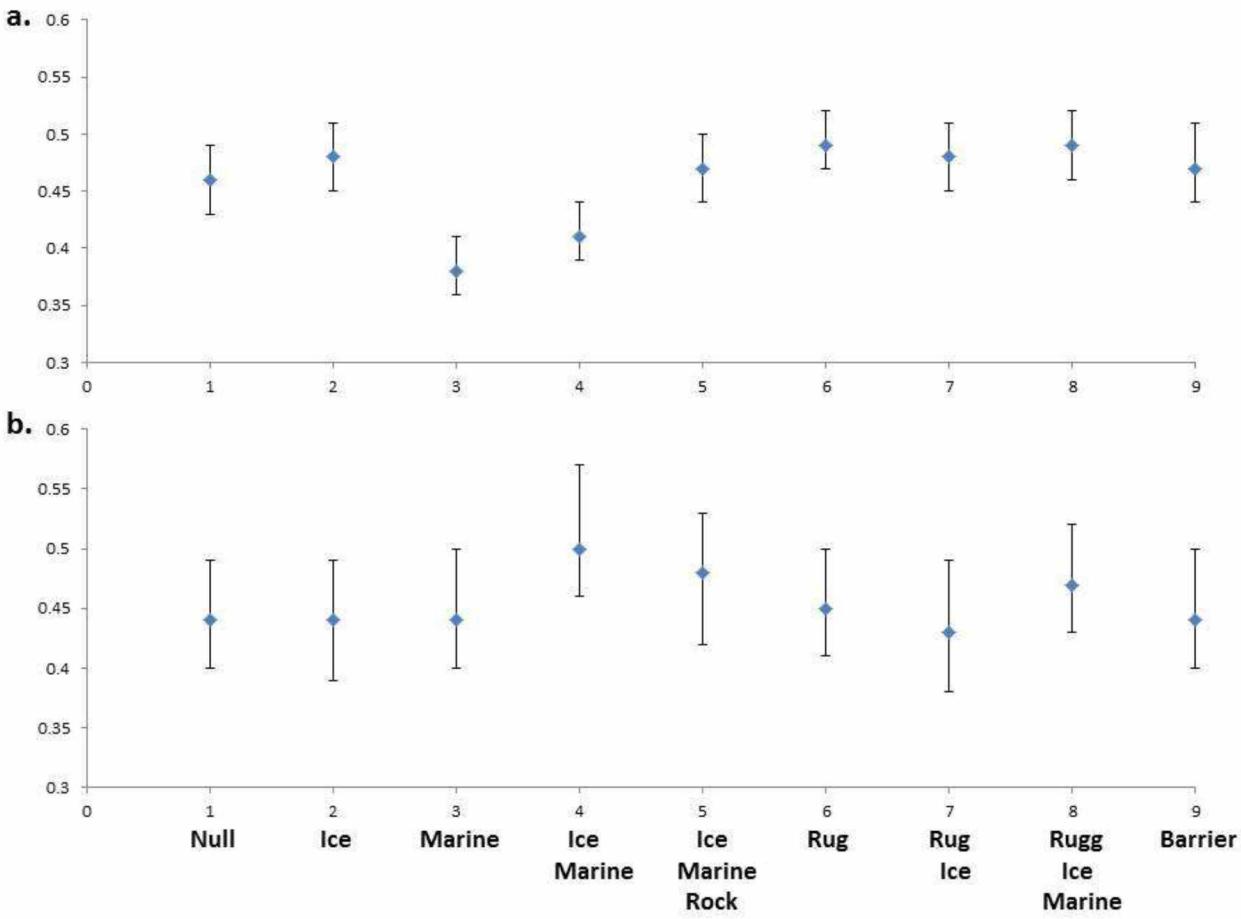


Fig. 2.12. Plot of Mantel r-values of landscape genetics correlations between genetic relatedness and landscape models for 105 brown bears in Glacier Bay, Alaska 2009-2010 using a) cost-distance all bears, and b) least-cost paths for females only. Bars represent 95% confidence intervals. All models were significant at $p<0.001$.

Table 2.1. Landscape models tested using cost-distance and least-cost paths. Isolation by Distance (IBD), Isolation by Resistance (IBR), and Isolation by Barrier (IBB) models were tested in ArcGIS Landscape Genetics at 200m cell resolution for brown bears in landscape genetics study, Glacier Bay, Alaska 2009-2010.

Model Name	Resistance Values	Methods/Source
IBD		
Eucl_Dist	No resistance values.	Euclidean distance between sample locations generated with Landscape Genetics extension for ArcGIS.
IBR		
Ice	Ice = 100 All other cells = 1	Unvegetated ice and snow from landcover layer (Albert and Schoen 2006)
Ice_mar	Ice and marine = 100 All other cells = 1	Unvegetated ice and snow from landcover layer (Albert and Schoen 2006) Marine layer from NOAA bathymetry layer.
Mar	Marine = 100 All other cells = 1	Marine extent from NOAA bathymetry layer
Ice_mar_rk	Ice and marine = 100 Rock = 50 All other cells = 1	Unvegetated ice and snow from landcover layer (Albert and Schoen 2006) Marine layer from NOAA bathymetry layer.
Rug	1) 1.00-1.07 = 1 2) 1.08-1.21 = 25 3) 1.22-1.40 = 50 4) 1.41-1.73 = 75 5) 1.74-5.89 = 100	Ratio of surface area of grid cell / by the planimetric area using GIS extension DEM Surface Tools v.2.1.254 (Jenness 2010a) categorized and scaled from 1-100.
Rug_ice	Cell values 1, 20, 40, 60, 80 and 100	Rugosity values (1-5) and ice model cell values (1, 50, and 100) multiplied and scaled proportionally from 1-100.
Rug_ice_mar	Cell values 1, 20, 40, 60, 80 and 100	Rugosity values (1-5) and ice_mar model cell values (1, 50, and 100) multiplied and scaled proportionally from 1-100.
IBB		
Barrier	Barrier cells = 1000 All other cells = 1	Single polylines drawn up the middle of lower Glacier Bay and through the Fairweather and Chilkat Mountains buffered to 5 km.

Table 2.2. Summary of genetic measures by sampling region for 105 brown bears in Glacier Bay, Alaska 2009-2010: sample size (N), no. alleles (Na), no. effective alleles (Ne), allelic richness (A), observed heterozygosity (Ho), unbiased expected heterozygosity (He), and Fixation Index (F). Bold type indicates the highest value per metric.

Population		N	Na	Ne	A	Ho	He	F
East GB	Mean	7	4.333	3.025	3.951	0.727	0.701	-0.118
	SE		0.187	0.166	0.156	0.037	0.022	0.041
Icy East	Mean	10	4.524	3.224	3.818	**0.762**	0.699	-0.151
	SE		0.203	0.191	0.157	0.036	0.024	0.044
Icy West	Mean	13	5.143	3.206	3.907	0.685	0.692	-0.040
	SE		0.232	0.183	0.161	0.027	0.023	0.038
West GB	Mean	**49**	**6.667**	**3.840**	4.131	0.737	0.721	**-0.026**
	SE		0.347	0.230	0.162	0.031	0.024	0.018
Yakutat	Mean	21	5.429	3.620	4.033	0.735	0.723	-0.045
	SE		0.245	0.200	0.144	0.026	0.019	0.031
Haines	Mean	5	4.286	3.341	**4.286**	0.752	**0.760**	-0.111
	SE		0.209	0.191	0.209	0.039	0.017	0.064
Total	Mean	17	5.063	3.376	4.284	0.733	0.716	-0.082
	SE	1.331	0.122	0.082	0.139	0.013	0.009	0.017

Table 2.3. Population assignments and proportion of ancestry of bears by sampling regions and number (and proportion) of admixed ($q < 0.8$) individuals brown bears by genetic group from program Structure, (a) and Geneland (b) at K=3 for 105 brown bears in Glacier Bay, Alaska 2009-2010. Bold font indicates the population the sample area was assigned based on the majority of ancestry of all bears combined.

a) Structure K = 2

Sample Area	West	East	n	Assigned Population
East GB	0.25	**0.75**	7	East
Icy East	0.04	**0.96**	10	East
Icy West	**0.79**	0.21	13	West
West GB	0.09	**0.91**	49	East
Yakutat	**0.91**	0.09	21	West
Haines	0.13	**0.87**	5	East
n	**35**	**70**	**105**	
Admixed	1(0.03)	6(0.09)	7(0.07)	

b) Structure K = 3

Sample Area	West	GLBA	East	n	Assigned Population
East GB	0.18	0.31	**0.51**	7	East
Icy East	0.02	0.02	**0.96**	10	East
Icy West	**0.78**	0.07	0.15	13	West
West GB	0.09	**0.53**	0.38	49	GLBA
Yakutat	**0.90**	0.03	0.07	21	West
Haines	0.05	0.02	**0.93**	5	East
n	**35**	**29**	**41**	**105**	
Admixed	2(0.06)	5(0.17)	6(0.15)	13(0.12)	

Table 2.3 continued.

c) Geneland K = 3

Sample Area	West	GLBA	East	n	Assigned Population
East GB	0.00	**1.00**	0.00	7	GLBA
Icy East	0.00	0.00	**1.00**	10	East
Icy West	**1.00**	0.00	0.00	13	West
West GB	0.00	**0.82**	0.18	49	GLBA
Yakutat	**0.95**	0.00	0.05	21	West
Haines	0.00	0.00	**1.00**	5	East
n	**33**	**47**	**25**	**105**	
Admixed	1(0.03)	8(0.17)	1(0.03)	10(0.10)	

Table 2.4. Pairwise Jost D values (below diagonal) and F_{st} values (above diagonal) for 105 brown bears in Glacier Bay, Alaska 2009-2010 by sampling areas (a) and by population (b). Bold font indicates significant ($p<0.05$) values.

a)

	East GB	Icy East	Icy West	West GB	Yakutat	Haines
East GB	-	**0.028**	**0.053**	0.016	**0.047**	0.040
Icy East	0.054	-	**0.075**	**0.052**	**0.083**	0.016
Icy West	**0.125**	**0.174**	-	**0.047**	0.016	0.038
West GB	0.029	**0.132**	**0.136**	-	**0.051**	0.023
Yakutat	**0.111**	**0.211**	0.043	**0.148**	-	**0.039**
Haines	**0.090**	0.003	**0.088**	0.061	**0.103**	-

b)

	West	East	GLBA
West	-	**0.051**	**0.050**
East	**0.165**	-	**0.022**
GLBA	**0.195**	**0.127**	-

Table 2.5. Summary of genetic measures by population for 105 brown bears in Glacier Bay, Alaska 2009-2010 across populations: sample size (N), no. alleles (Na), no. effective alleles (Ne), rarefacted allelic richness (A), observed heterozygosity (Ho), unbiased expected heterozygosity (He), and number of private alleles (PA). Bold type indicates the highest value per metric.

Population		N	Na	Ne	A	Ho	He	PA
West	Mean	35	5.762	3.468	6.367	0.710	0.706	9
	SE		0.217	0.179	0.311	0.021	0.017	
East	Mean	**41**	**6.762**	**3.893**	**6.502**	**0.758**	**0.738**	**21**
	SE		0.330	0.202	0.299	0.019	0.015	
GLBA	Mean	29	5.000	3.316	6.142	0.724	0.675	2
	SE		0.331	0.198	0.344	0.040	0.035	

Conclusions

Distribution

Black bears have colonized lower and mid bay and are strongly associated with closed forest. Black bear distributions will likely move northward with the forest succession. Black and brown bear distributions overlap much more than previously believed, but competition between the species could not be inferred based on occupancy models. Brown bears have completely colonized Glacier Bay, but frequency of use may be higher in open scrub and herbaceous vegetation and lower in young forest. Recent increase in sightings of brown bears in the southern bay and town of Gustavus indicate that the colonization of these areas is recent, and may signify a second pulse of colonization. Anecdotal sightings show that brown bears have been rare in southern Glacier Bay for over 50 years, indicating a possible successional state in which brown bears cannot obtain food resources needed to support their large body size. Young forest of the southern bay may just be emerging from this period and brown bears moving back in, while the recently deglaciated areas may have yet to reach this successional stage at which time brown bear use may decline. All sightings if brown bears in southern Glacier Bay were of single bears and no family groups have yet been documented, indicating that successful colonization in these areas may have not yet occurred.

Brown bear landscape genetics

The shoreline of Glacier Bay hosts brown bears from three distinct populations. The ranges of two of these populations (East and West) extend well into non-park lands to the Northeast and Northwest, while the range of the third population (Glacier Bay, or GLBA) is specific to the park. The GLBA group is likely composed of the original colonizers that were isolated long enough to undergo genetic drift. Immigration into Glacier Bay is recent and ongoing indicating possibly a second wave of colonization. Genetic introgression is likely, especially in northern Glacier Bay where the three populations overlap. Resistance models (IBR) were correlated with genetic relatedness, but not

significantly more than barrier (IBB) or distance models (IBD). Correlations between landscape models and least-cost paths of females only differed from cost-paths of all bears, indicating different landscape features influencing genetic connectivity between the sexes although not significantly. The southern portion of Glacier Bay fjord appears to be a barrier to dispersal, thus perpetuating the East/West genetic divide. The Fairweather Mountain range appears to further impede dispersal on the west side of Glacier Bay, as indicated by genetic differentiation between bears of Glacier Bay vs. Yakutat forelands. As the ice retreated from the south after the LIA, bears as well as other animals likely recolonized newly available terrain from both east and west refugia while Glacier Bay fjord inhibited movement of terrestrial species across the bay and funneled dispersal in a northward direction. At the northern end of Glacier Bay these populations came into secondary contact after several hundreds of years of separation, creating a biological suture zone at population levels.

Further Research

Abundance estimates in areas of management concern

The methods used in this study for genetic detection of black and brown bears could be used to develop population estimates using mark-recapture techniques in areas of management concern. Genotyping success of hair samples could be improved by frequent repeated sampling of rub tree locations, as well as deploying scented hair traps. Areas of management concern include the Gustavus forelands and the National Preserve, where hunting is allowed and bears undoubtedly move in and out of protected park lands.

Projecting future distributions of black and brown bears

The occupancy model generated for black bears could be used to project future distribution given projected forest cover models. Similarly, brown bear use, although not occupancy, could be projected based on the future landcover models.

Resource partitioning between species

To further explore competition between black and brown bear species, comparing dietary components of both species could be conducted using stable isotope analysis of hair collected in this study. Differences in diet of both species between areas where sympatric and allopatric may indicate competition for food resources and determine if dietary segregations occurs.

Larger regional analysis of brown bear population structure

A regional population structure analysis of brown bears is warranted given the recent glacial history and extreme topography of northern Southeast Alaska combined with the newly discovered population substructure of brown bears in the Glacier Bay area. Colonization of new areas by brown bears is active and current in this region, and determination of landscape features that limit brown bear genetic connectivity in a region with very little human development may help differentiate natural from anthropogenic fragmentation in disturbed landscapes.

Black bear population structure and glacier bear genetic basis

Population and landscape genetics analysis of black bears in the Glacier Bay region would be interesting to determine landscape influences on genetic connectivity of this species, as well as the genetic basis for the rare glacier bear. The Glacier Bay region appears to be the range center of glacier bears (or blue bears), an uncommon color variants of black bears whose pelage ranges from white to black with silver hair tips. Currently there is very little scientific knowledge of the genetic basis or the frequency of this unusual pelage color making it difficult to manage and predict the future survival of glacier bears.

Explore possible suture zone

Population structure across multiple mammalian taxa and taxonomic levels would provide insight into the hypothesis that northern Glacier Bay is a biological suture zone

resulting from ice retreat after the LIA. Since hunting is not allowed in the park, non-invasive sampling techniques will need to be developed and/or carried out for many species.

Further biogeographic research

Rapid glacial retreat in Glacier Bay has led to progressive exposure of new land surface and subsequent plant and animal colonization has greatly altered ecological composition on this landscape. Species such must adapt rapidly (e.g. within decade or less) to abrupt changes in food types and abundance. For this reason, Glacier Bay can serve as a model for climate change where physical and biological processes resulting from warming trends can be observed over a relatively short period of time. Additionally, the recent glacial history and rugged landscape provides an opportunity to observe recolonization patterns of plants and animals after the LIA, which in turn can lead to insights on recolonization of the entire region after the LGM.